

University of Alberta

Landscape Ecology of Mule Deer (*Odocoileus hemionus*) and White-tailed
Deer (*O. virginianus*) with Implications for Chronic Wasting Disease

by

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ABSTRACT

Chronic wasting disease (CWD) is a fatal prion disease of cervids that continues to spread into new regions of Canada despite containment efforts. I examine the importance of landscape connectivity using circuit theory and source/sink habitats that are based on selection, survival and reproduction in order to assess CWD spread risk among deer in Alberta, Canada. I found for hunter-harvested deer that the likelihood of being CWD-positive was higher for mule deer than white-tailed deer and for deer in habitat associated with river drainages and areas more connected to previously detected CWD-positive deer. Source habitats differed between the two species primarily due to differences in habitat selection, with consequences for reproduction and hunting mortality in mule deer and natural mortality in white-tailed deer. My results will help wildlife managers prioritize areas for CWD monitoring and control, as well as contribute to the development of future spatially explicit disease spread models.

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CHAPTER 1

INTRODUCTION

Wildlife diseases impact economies, human health and biodiversity. As a result it is important to understand disease processes in order to implement effective control and mitigation strategies (Thirgood 2009). Examining spatial disease patterns is an important first step to understanding disease dynamics because it relates the environment to host, vector and pathogen distribution, which determines the spatial variation in disease risk and occurrence (Ostfeld *et al.* 2005). From a management perspective relating disease occurrence to environmental factors has been used to prioritize areas for control or conservation. For example, Gahl & Calhoun (2008) modeled the occurrence of Ranavirus, a fatal amphibian infection, as a function of wetland proximity to other infected wetlands and catchment position. They found that infection risk increased with catchment height and prioritized these areas for control efforts. Once a better understanding of the underlying disease process is known, spatially explicit models can be used to test different control and management strategies prior to implementation (Gewin 2004; Lange *et al.* 2012). For example, Smith & Wilkinson (2003) used a spatial stochastic simulation model of rabies in a red fox population to test the effectiveness of culling versus fertility control and vaccination at disease eradication. They found that, when fox densities were low, all options were equally as effective but, when densities were high, culling was optimal. The best disease control strategy depends on the ability of the disease to

spread (i.e. spread rate and directionality) and the transmission rate within host populations (Tildesley *et al.* 2009; Woolhouse 2011; Keeling & Shattock 2012).

Landscape heterogeneity influences the spatial dynamics of infectious disease, particularly the likelihood of introduction into naive populations and the propagation of disease within a population. The spread of disease can be represented as a wave of infection moving across the landscape driven by the movement of infected individuals into new regions (Murray *et al.* 1986; Lewis *et al.* 2006). If the host or vector is impeded by landscape features, like large rivers or mountain ranges, then the progression of the wave will be slowed or even halted (Smith *et al.* 2002; Russell *et al.* 2004; Cullingham *et al.* 2009). The result is an irregular disease front with some populations becoming infected earlier than others (Hastings *et al.* 2005; Garlick *et al.* 2011). After introduction, the host population size and demographics controls the transmission and continuation of infection (Grenfell & Dobson 1995; Thrusfield 2007). If contacts are density dependent then a disease is more likely to perpetuate in a larger population because there may be greater contact between infected and susceptible individuals, which increases transmission likelihood (Dobson & Hudson 1995; Begon *et al.* 2002; Begon *et al.* 2003). Also, there is a continual replenishment of new susceptible hosts that reduces the chance of disease extinction (Grenfell & Harwood 1997; Grenfell & Bolker 1998; Acosta-Jamett *et al.* 2010). Ultimately host demography is a result of the rate of mortality and reproduction within the population (Sibly & Hone 2003), which is influenced by habitat quality and landscape attributes (McLoughlin *et al.* 2006; McLoughlin *et al.* 2007; Panzacchi

et al. 2009). Therefore disease dynamics are impacted by the landscape heterogeneity via host habitat quality and the rate and propensity of disease spread into new regions.

Recently, chronic wasting disease (CWD), a prion disease of cervids, has emerged among many wild cervid populations in North America resulting in risk for environmental and economic impacts (Detwiler *et al.* 2000). CWD is an invariably fatal disease with no known vaccination or treatment (Williams *et al.* 2002). The mechanism of transmission in the wild is unclear but likely involves both direct (animal to animal) and indirect (animal to environment to animal) transmission (Miller *et al.* 2006; Mathiason *et al.* 2009; Gough & Maddison 2010). CWD is capable of being transmitted between cervid species, resulting in infections among: white-tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), elk (*Cervus canadensis*) and moose (*Alces alces*, Williams *et al.* 2002; Baeten *et al.* 2007). The disease was first documented in Colorado and Wyoming in the 1960-70s (Williams & Young 1980). Managers in these two states responded by trying to limit the spread of the disease into new areas by reducing prevalence in enzootic areas through increased hunter-harvest and strategic herd reductions (Peterson *et al.* 2002; Wyoming Game and Fish Commission 2006). However, CWD has since spread or been translocated to an additional 18 U.S. states and 2 Canadian provinces (Chronic Wasting Disease Alliance 2012). In these affected regions CWD is a concern because it can affect deer populations by decreasing survival rates and recruitment (Dulberger *et al.* 2010; Sargeant *et al.* 2011). Additionally, while humans are probably not

susceptible, it is still a health concern (MaWhinney *et al.* 2006) and it increases costs for cervid farms (Arnot *et al.* 2009). Therefore, CWD has become an important management issue throughout much of North America.

Alberta (AB) and Saskatchewan (SK) are currently managing CWD outbreaks in wild mule and white-tailed deer populations. The timing and locations of CWD discovery in these adjacent provinces suggests that they are related epidemics. Both AB and SK were proactive in CWD surveillance beginning in 1998 and 1997 respectively (Alberta Environment and Sustainable Resource Development 2012; Saskatchewan Ministry of Environment 2011). The first case among wild deer was found in SK in 2000 and was likely the result of spill over from infected game farms (Bollinger *et al.* 2004). In 2005, Alberta discovered its first case near the AB-SK border in the South Saskatchewan River drainage adjacent to positive cases in SK (Alberta Sustainable Resource Development 2012). CWD likely spread from SK into AB via the dispersal and migration of infected deer. To date there has been 127 cases in AB and 311 cases in SK in both mule and white-tailed deer (Alberta Environment and Sustainable Resource Development 2012; Saskatchewan Ministry of Environment 2011). Both provinces have focused on reducing deer densities for disease control by increasing hunter-harvest, with Alberta instituting a herd reduction program from 2005-2008 (Pybus 2006; Pybus 2007). However, complete eradication of the disease is unlikely in either province (Canadian Cooperative Wildlife Health Centre 2011). Limiting the spread farther westward into Alberta may still be possible (Langenberg *et al.* 2008; Pybus 2012). Reducing spread is difficult

because there are no apparent barriers to CWD spread in AB and SK (Cullingham *et al.* 2011; Cullingham *et al.* 2011). As a result there is significant need for a model to predict high risk areas for CWD introduction so managers can proactively target these sites with surveillance and control measures to increase the likelihood of containing further disease spread.

The movement of deer is important to the spread of CWD in wild populations (Conner & Miller 2004; Oyer *et al.* 2007; Skuldt *et al.* 2008). Both mule and white-tailed deer, the primary hosts of CWD in Alberta, are migratory and known to disperse distances > 40 km (Diefenbach *et al.* 2008; Clements *et al.* 2011). Landscape characteristics can affect deer movement, for example pursued mule deer move up slopes to avoid predators, while white-tailed deer tend to travel on gentle terrain (Lingle 2002). Deer movement paths, observed via GPS collars, avoid human development like domiciles (Coulon *et al.* 2008), roads (Fortin *et al.* 2005) and well sites (Sawyer *et al.* 2009). Because deer movements are influenced by landscape characteristics, the connectivity between areas will influence the probability of dispersal (Long *et al.* 2005; Skuldt *et al.* 2008; Long *et al.* 2010) and disease spread (Blanchong *et al.* 2008; Schreiber & Lloyd-Smith 2009). Despite the suspected importance of deer movement to disease spread, there has been no incorporation of deer movement or landscape connectivity into CWD risk models (but see Garlick *et al.* 2011) and no evaluation of whether connectivity better relates to disease occurrence than Euclidian distance.

CWD spread is not only determined by deer movement but also by landscape features that influence disease propagation post-introduction, which is

determined by deer densities and contacts rates between infected and susceptible individuals (Begon *et al.* 2002; Miller & Williams 2003; Miller *et al.* 2006). For example, in Wisconsin and Colorado respectively, prevalence was related to amount of forest cover (Joly *et al.* 2006) and human development (Farnsworth *et al.* 2005), which likely correlate with deer densities. High deer densities cause an increase in home range overlap and more direct and indirect contact (Habib *et al.* 2011). Within a home range, pair-wise contacts between GPS-collared deer have been shown to be disproportionately higher in forest cover and agriculture habitat important to deer (Kjaer *et al.* 2008; Habib *et al.* 2011; Silbernagel *et al.* 2011). River drainages are likely sites for indirect contact in a prairie river ecosystem because it is frequented by many deer for bedding and escape cover (Silbernagel *et al.* 2011). Survival and recruitment rates have been shown to be important to prevalence and likelihood of CWD eradication in non-spatial simulations (Potapov *et al.* 2012). Although spatial disease models have focused on relating CWD prevalence or occurrence to landscape characteristics (Joly *et al.* 2006; Farnsworth *et al.* 2005; Rees *et al.* 2012), there has been no incorporation of spatial variation in vital rates into spatial CWD models. This is because there needs to be a greater understanding of how deer habitat impacts survival and reproduction in a CWD infected population.

In Chapter 2, I contrast between CWD-positive and negative deer their local landscape features, species, sex and landscape connectivity to previously detected CWD cases to identify factors important to the CWD occurrence. Landscape connectivity was quantified based on the habitat selection displayed by traveling

deer (Fortin *et al.* 2005) combined with a circuit theory approach (McRae *et al.* 2008). The resulting risk model is among the first to incorporate landscape connectivity into predictions of disease spread in a wild population, but unlike previous studies (Bar-David *et al.* 2006; Remais *et al.* 2010; Garlick *et al.* 2011), connectivity was compared to a null model representing Euclidian distances. The CWD risk model was then used to assess and map the likelihood of CWD occurrence in wildlife management units where CWD had not been detected but were at risk of disease introduction by being adjacent to known disease foci.

In Chapter 3, I compare the spatial distribution of source and sink habitat for female mule and white-tailed deer as a first step in assessing their contribution to disease transmission and spread. I combined seasonal habitat selection with probabilities of pregnancy and mortality resulting from habitat use (Nielsen *et al.* 2006). Habitat selection was modeled based on the locations of GPS-collared deer using a resource selection probability function (Lele 2009). The relationship between habitat and pregnancy rates was modeled based on pregnancy data collected from female deer harvested during the CWD herd reduction program. I quantified the spatial variation in mortality risk with a Cox proportional hazard model (Cox 1972) using locations and mortalities of VHF and GPS-collared deer. Source-sink habitat was classified specifically for: 1) pregnancy rates in the summer, 2) mortality risk from hunting in the fall and 3) natural mortality risk throughout the year. The three source habitat classifications and habitat selection alone were compared to winter deer densities to determine which best predicted deer densities.

In Chapter 4, I summarize the results and discuss implications and suggestions for the management of deer populations and controlling CWD.

Literature Cited

- Acosta-Jamett, G., Cleaveland, S., Cunningham, A.A. & Bronsvoort, B.M. (2010) Demography of domestic dogs in rural and urban areas of the coquimbo region of chile and implications for disease transmission. *Preventive Veterinary Medicine*, **94**, 272-281.
- Alberta Environment and Sustainable Resource Development. (2011) Statistics: Chronic Wasting Disease in Wild Deer in Alberta (2011). <http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/CWDUpdates/Default.aspx> [Accessed 1 June 2011]
- Alberta Environment and Sustainable Resource Development. (2012) CWD History in Alberta. <http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/CWDUpdates/CWDHistoryinAlberta.aspx> [Accessed 3 September 2012]
- Arnot, C., Laate, E., Unterschultz, J. & Adamowicz, W. (2009) Chronic wasting disease (CWD) potential economic impact on cervid farming in alberta. *Journal of Toxicology and Environmental Health-Part A-Current Issues*, **72**, 1014-1017.
- Baeten, L.A., Powers, B.E., Jewell, J.E., Spraker, T.R. & Miller, M.W. (2007) A natural case of chronic wasting disease in a free-ranging moose (alces alces shirasi). *Journal of Wildlife Diseases*, **43**, 309-314.
- Bar-David, S., Lloyd-Smith, J.O. & Getz, W.M. (2006) Dynamics and management of infectious disease in colonizing populations. *Ecology*, **87**, 1215-1224.
- Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M. & Turner, J. (2002) A clarification of transmission terms in host-microparasite models: Numbers, densities and areas. *Epidemiology and Infection*, **129**, 147-153.
- Begon, M., Hazel, S., Telfer, S., Bown, K., Carslake, D., Cavanagh, R., Chantrey, J., Jones, T. & Bennett, M. (2003) Rodents, cowpox virus and islands: Densities, numbers and thresholds. *Journal of Animal Ecology*, **72**, 343-355.
- Blanchong, J.A., Samuel, M.D., Scribner, K.T., Weckworth, B.V., Langenberg, J.A. & Filcek, K.B. (2008) Landscape genetics and the spatial distribution of chronic wasting disease. *Biology Letters*, **4**, 130-133.
- Bollinger, T., Caley, P., Merrill, E.H., Messier, F., Miller, M.W., Samuel, M.D. & Vanopdenbosch, E. (2004) Expert scientific panel on chronic wasting disease. chronic wasting disease in canadian wildlife: An expert opinion on

the epidemiology and risk to wild deer. *Canadian Cooperative Wildlife Health Centre*.

- Canadian Cooperative Wildlife Health Centre. (2011) A Proposal for Canada's National Chronic Wasting Disease Control Strategy. http://www.ccwhc.ca/publications/A_Proposal_for_a_National_CWD_Control_Strategy_2011_final.pdf
- Chronic Wasting Disease Alliance. (2012) CWD found in deer at Iowa hunting preserve. *News and Updates*, <http://www.cwd-info.org/index.php/fuseaction/news.detail/ID/8c3867db5ac6a710615358166ad79b23> [Accessed 1 August 2012]
- Clements, G.M., Hygnstrom, S.E., Gilsdorf, J.M., Baasch, D.M., Clements, M.J. & Vercauteren, K.C. (2011) Movements of white-tailed deer in riparian habitat: Implications for infectious diseases. *Journal of Wildlife Management*, **75**, 1436-1442.
- Conner, M.M. & Miller, M.W. (2004) Movement patterns and spatial epidemiology of a prion disease in mule deer population units. *Ecological Applications*, **14**, 1870-1881.
- Coulon, A., Cosson, J.F., Angibault, J.M., Cargnelutti, B., Galan, M., Morellet, N., Petit, E., Aulagnier, S. & Hewison, A.J.M. (2004) Landscape connectivity influences gene flow in a roe deer population inhabiting a fragmented landscape: An individual-based approach. *Molecular Ecology*, **13**, 2841-2850.
- Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J. & Hewison, A.J.M. (2008) Inferring the effects of landscape structure on roe deer (*capreolus capreolus*) movements using a step selection function. *Landscape Ecology*, **23**, 603-614.
- Cox, D.R. (1972) Regression models and life-tables. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **34**, 187-193.
- Cullingham, C.I., Nakada, S.M., Merrill, E.H., Bollinger, T.K., Pybus, M.J. & Coltman, D.W. (2011) Multiscale population genetic analysis of mule deer (*odocoileus hemionus hemionus*) in western canada sheds new light on the spread of chronic wasting disease. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **89**, 134-147.
- Cullingham, C.I., Kyle, C.J., Pond, B.A., Rees, E.E. & White, B.N. (2009) Differential permeability of rivers to raccoon gene flow corresponds to rabies incidence in ontario, canada. *Molecular Ecology*, **18**, 43-53.

- Cullingham, C.I., Merrill, E.H., Pybus, M.J., Bollinger, T.K., Wilson, G.A. & Coltman, D.W. (2011) Broad and fine-scale genetic analysis of white-tailed deer populations: Estimating the relative risk of chronic wasting disease spread. *Evolutionary Applications*, **4**, 116-131.
- Detwiler, L.A., Rubenstein, R. & Williams, E.S. (2000) Transmissible spongiform encephalopathies. *Emerging Diseases of Animals* (eds C. Brown & C. Bolin), pp. 131-160. Washington, D.C, ASM Press.
- Diefenbach, D.R., Long, E.S., Rosenberry, C.S., Wallingford, B.D. & Smith, D.R. (2008) Modeling distribution of dispersal distances in male white-tailed deer. *Journal of Wildlife Management*, **72**, 1296-1303.
- Dobson, A.P. & Hudson, P.J. (1995) Microparasites: Observed patterns in wild animal populations. *Ecology of Infectious Diseases in Natural Populations* (eds B.T. Grenfell & A.P. Dobson), pp. 52-89. Cambridge; New York, Cambridge University Press.
- Dulberger, J., Hobbs, N.T., Swanson, H.M., Bishop, C.J. & Miller, M.W. (2010) Estimating chronic wasting disease effects on mule deer recruitment and population growth. *Journal of Wildlife Diseases*, **46**, 1086-1095.
- Farnsworth, M.L., Wolfe, L.L., Hobbs, N.T., Burnham, K.P., Williams, E.S., Theobald, D.M., Conner, M.M. & Miller, M.W. (2005) Human land use influences chronic wasting disease prevalence in mule deer. *Ecological Applications*, **15**, 119-126.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in yellowstone national park. *Ecology*, **86**, 1320-1330.
- Gahl, M.K. & Calhoun, A.J.K. (2008) Landscape setting and risk of ranavirus mortality events. *Biological Conservation*, **141**, 2679-2689.
- Garlick, M.J., Powell, J.A., Hooten, M.B. & McFarlane, L.R. (2011) Homogenization of large-scale movement models in ecology. *Bulletin of Mathematical Biology*, **73**, 2088-2108.
- Geist, V. (1981) Behavior: Adaptive strategies in mule deer. *Mule and Black-Tailed Deer of North America* (ed O. Wallmo), pp. 605. Lincoln, Nebraska, University of Nebraska Press.
- Gewin, V. (2004) Disease control: Virtual plagues get real. *Nature*, **427**, 774-775.
- Gough, K.C. & Maddison, B.C. (2010) Prion transmission prion excretion and occurrence in the environment. *Prion*, **4**, 275-282.

- Grenfell, B. & Harwood, J. (1997) (Meta)population dynamics of infectious diseases. *Trends in Ecology & Evolution*, **12**, 395-399.
- Grenfell, B.T. & Bolker, B.M. (1998) Cities and villages: Infection hierarchies in a measles metapopulation. *Ecology Letters*, **1**, 63-70.
- Grenfell, B.T. & Dobson, A.P. eds. (1995) Ecology of infectious diseases in natural populations. *Publications of the Newton Institute*. 7 Anonymous pp. 521. Cambridge; New York, Cambridge University Press.
- Habib, T.J., Merrill, E.H., Pybus, M.J. & Coltman, D.W. (2011) Modelling landscape effects on density-contact rate relationships of deer in eastern alberta: Implications for chronic wasting disease. *Ecological Modelling*, **222**, 2722-2732.
- Hastings, A., Cuddington, K., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A., Harrison, S., Holland, M., Lambrinos, J., Malvadkar, U., Melbourne, B.A., Moore, K., Taylor, C. & Thomson, D. (2005) The spatial spread of invasions: New developments in theory and evidence. *Ecology Letters*, **8**, 91-101.
- Joly, D.O., Samuel, M.D., Langenberg, J.A., Blanchong, J.A., Batha, C.A., Rolley, R.E., Keane, D.P. & Ribic, C.A. (2006) Spatial epidemiology of chronic wasting disease in wisconsin white-tailed deer. *Journal of Wildlife Diseases*, **42**, 578-588.
- Keeling, M.J. & Shattock, A. (2012) Optimal but unequitable prophylactic distribution of vaccine. *Epidemics*, **4**, 78-85.
- Kjaer, L.J., Schaub, E.M. & Nielsen, C.K. (2008) Spatial and temporal analysis of contact rates in female white-tailed deer. *Journal of Wildlife Management*, **72**, 1819-1825.
- Lange, M., Kramer-Schadt, S. & Thulke, H. (2012) Efficiency of spatio-temporal vaccination regimes in wildlife populations under different viral constraints. *Veterinary Research*, **43**, 37.
- Langenberg, J.A., Miller, M.W. & Creekmore, L. (2008) *Alberta Chronic Wasting Disease Management Program Review Panel Report*.
<http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/documents/AlbertaCWDMManagement-ProgramReviewPanelReport-Feb2008.pdf>
- Lele, S.R. (2009) A new method for estimation of resource selection probability function. *Journal of Wildlife Management*, **73**, 122-127.

- Lewis, M., Renclawowicz, J. & Van den Driessche, P. (2006) Traveling waves and spread rates for a west Nile virus model. *Bulletin of Mathematical Biology*, **68**, 3-23.
- Lingle, S. (2003) Group composition and cohesion in sympatric white-tailed deer and mule deer. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **81**, 1119-1130.
- Lingle, S. (2002) Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, **83**, 2037-2048.
- Long, E.S., Diefenbach, D.R., Rosenberry, C.S., Wallingford, B.D. & Grund, M.R.D. (2005) Forest cover influences dispersal distance of white-tailed deer. *Journal of Mammalogy*, **86**, 623-629.
- Long, E.S., Diefenbach, D.R., Wallingford, B.D. & Rosenberry, C.S. (2010) Influence of roads, rivers, and mountains on natal dispersal of white-tailed deer. *Journal of Wildlife Management*, **74**, 1242-1249.
- Mathiason, C.K., Hays, S.A., Powers, J., Hayes-Klug, J., Langenberg, J., Dahmes, S.J., Osborn, D.A., Miller, K.V., Warren, R.J., Mason, G.L. & Hoover, E.A. (2009) Infectious prions in pre-clinical deer and transmission of chronic wasting disease solely by environmental exposure. *Plos One*, **4**, 5916-5934.
- MaWhinney, S., Pape, W.J., Forster, J.E., Anderson, C.A., Bosque, P. & Miller, M.W. (2006) Human prion disease and relative risk associated with chronic wasting disease. *Emerging Infectious Diseases*, **12**, 1527-1535.
- McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1449-1454.
- McLoughlin, P.D., Gaillard, J.-., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Said, S. & Klein, F. (2007) Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192-3201.
- McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, **89**, 2712-2724.
- Miller, M.W. & Conner, M.M. (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. & Williams, E.S. (2003) Horizontal prion transmission in mule deer. *Nature*, **425**, 35-36.
- Miller, M.W., Hobbs, N.T. & Tavener, S.J. (2006) Dynamics of prion disease transmission in mule deer. *Ecological Applications*, **16**, 2208-2214.
- Murray, J.D., Stanley, E.A. & Brown, D.L. (1986) On the spatial spread of rabies among foxes. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **229**, 111-150.
- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in alberta. *Biological Conservation*, **130**, 217-229.
- Ostfeld, R.S., Glass, G.E. & Keesing, F. (2005) Spatial epidemiology: An emerging (or re-emerging) discipline. *Trends in Ecology & Evolution*, **20**, 328-336.
- Oyer, A.M., Mathews, N.E. & Skuldt, L.H. (2007) Long-distance movement of a white-tailed deer away from a chronic wasting disease area. *Journal of Wildlife Management*, **71**, 1635-1638.
- Panzacchi, M., Linnell, J.D.C., Odden, M., Odden, J. & Andersen, R. (2009) Habitat and roe deer fawn vulnerability to red fox predation. *Journal of Animal Ecology*, **78**, 1124-1133.
- Peterson, M.J., Samuel, M.D., Nettles, V.F., Wobeser, G. & Hueston, W.D. (2002) Review of chronic wasting disease management policies and programs in colorado. *Colorado Wildlife Commission, Denver, Colorado, USA*, .
- Potapov, A., Merrill, E. & Lewis, M.A. (2012) Wildlife disease elimination and density dependence. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 3139-3145.
- Pybus, M. (2012) CWD Program Review. *Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta*.
<http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/documents/CWD-ProgramReview-May-2012.pdf>
- Pybus, M. (2007) *Alberta's Chronic Wasting Disease Response Program: March, 2007*. Alberta Sustainable Resource Development Internal Report.
- Pybus, M. (2006) *Alberta's Chronic Wasting Disease Management Programs in 2006 and upcoming surveillance*. Alberta Sustainable Resource Development Internal Report.

- Remais, J., Akullian, A., Ding, L. & Seto, E. (2010) Analytical methods for quantifying environmental connectivity for the control and surveillance of infectious disease spread. *Journal of the Royal Society Interface*, **7**, 1181-1193.
- Russell, C., Smith, D., Waller, L., Childs, J. & Real, L. (2004) A priori prediction of disease invasion dynamics in a novel environment RID B-2226-2008. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 21-25.
- Sargeant, G.A., Weber, D.C. & Roddy, D.E. (2011) Implications of chronic wasting disease, cougar predation, and reduced recruitment for elk management. *Journal of Wildlife Management*, **75**, 171-177.
- Saskatchewan Ministry of Environment. (2011) *Summary of the provincial CWD sampling effort 1997 - 2010*. Government of Saskatchewan. Updated March 21, 2011.
<http://www.environment.gov.sk.ca/adx/asp/adxGetMedia.aspx?DocID=d9171e89-a700-422b-864614c8c9abd466&MediaID=4918&Filename=Summary+of+Provincial+Sampling+Effort+1997-2010.pdf&l=English>. [Accessed 2 June 2011]
- Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, **73**, 1052-1061.
- Schreiber, S.J. & Lloyd-Smith, J.O. (2009) Invasion dynamics in spatially heterogeneous environments. *American Naturalist*, **174**, 490-505.
- Sibly, R.M. & Hone, J. (2003) Population growth rate and its determinants: An overview. *Wildlife Population Growth Rates* (eds R.M. Sibly, J. Hone & T.H. Clutton-Brock), pp. 11-40. Cambridge, U.K; New York, The Royal Society in association with Cambridge University Press.
- Silbernagel, E., Skelton, N., Waldner, C. & Bollinger, T. (2011) Interaction among deer in a chronic wasting disease endemic zone. *Journal of Wildlife Management*, **75**, 1453-1461.
- Skuldt, L.H., Mathews, N.E. & Oyer, A.M. (2008) White-tailed deer movements in a chronic wasting disease area in south-central wisconsin. *Journal of Wildlife Management*, **72**, 1156-1160.
- Smith, D.L., Lucey, B., Waller, L.A., Childs, J.E. & Real, L.A. (2002) Predicting the spatial dynamics of rabies epidemics on heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 3668-3672.

- Smith, G. & Wilkinson, D. (2003) Modeling control of rabies outbreaks in red fox populations to evaluate culling, vaccination, and vaccination combined with fertility control. *Journal of Wildlife Diseases*, **39**, 278-286.
- Thirgood, S. (2009) New perspectives on managing wildlife diseases. *Journal of Applied Ecology*, **46**, 454-456.
- Thrusfield, M.V. (2007) *Veterinary Epidemiology*, 3rd edn. Oxford, Blackwell.
- Tildesley, M.J., Bessell, P.R., Keeling, M.J. & Woolhouse, M.E.J. (2009) The role of pre-emptive culling in the control of foot-and-mouth disease. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3239-3248.
- Williams, E.S. & Young, S. (1980) Chronic wasting disease of captive mule deer - spongiform encephalopathy. *Journal of Wildlife Diseases*, **16**, 89-98.
- Williams, E.S., Miller, M.W., Kreeger, T.J., Kahn, R.H. & Thorne, E.T. (2002) Chronic wasting disease of deer and elk: A review with recommendations for management. *Journal of Wildlife Management*, **66**, 551-563.
- Woolhouse, M. (2011) How to make predictions about future infectious disease risks. *Philosophical Transactions of the Royal Society B-Biological Sciences*, **366**, 2045-2054.
- Wyoming Game and Fish Commission. (2006) *Wyoming game and fish department chronic wasting disease management plan*. <http://www.cwd-info.org/pdf/CWDPlanWY.pdf>

CHAPTER 2

PREDICTING THE RISK OF CHRONIC WASTING DISEASE IN EAST-CENTRAL ALBERTA

Introduction

Landscape connectivity is a fundamental component of many ecological processes. High connectivity between populations decreases the chances of localized extinction because populations can be rescued by immigration (Brown & Kodric-Brown 1977; Wilcox & Murphy 1985; Proctor *et al.* 2012). At the same time, high connectivity between populations may lead to declines in populations from lethally contagious diseases if connectivity facilitates pathogen movement (Hess 1994; Hess 1996). As a result, connectivity between disease sources are commonly incorporated into disease spread models (Hess *et al.* 2002). For example, for human diseases like severe acute respiratory syndrome (SARS), connectivity among individuals within a community can be established from interviews that form the basis of connections in social network models to explore outbreak potential (Meyers *et al.* 2005). Similarly, with livestock diseases like bovine tuberculosis, connectivity between farms can be quantified by tracking the human-mediated exchange of animals to inform models for predicting the likelihood of bovine tuberculosis introduction into an area (Gilbert *et al.* 2005).

In contrast, for wild animal populations, information is typically limited on what directs host movement, which hinders our ability to predict disease spread. As a result, Euclidian distance is used to represent the proximity of an area to

disease sources, and in a number of cases this metric has been found to be related to new cases or “sparks” in disease spread (Joly *et al.* 2006; Meentemeyer *et al.* 2008; Vaclavik *et al.* 2010; Rees *et al.* 2012). However, evidence also is accumulating that landscape features can bias host movements (Coulon *et al.* 2008; Sawyer *et al.* 2009; Roever *et al.* 2010; Clements *et al.* 2011; Gillies *et al.* 2011; La Morgia *et al.* 2011; McKenzie *et al.* 2012), which may cause directed disease spread (Smith *et al.* 2002; Russell *et al.* 2004; Blanchong *et al.* 2008; Schreiber & Lloyd-Smith 2009). As a result, few studies have used information on animal movements to predict disease spread (Bar-David *et al.* 2006; Garlick *et al.* 2011), but none have compared model outcomes with observed patterns in disease occurrence to determine whether landscape connectivity based on animal movement improved predictions of disease spread.

Chronic wasting disease (CWD) is a fatal prion disease of cervids (Williams *et al.* 2002) that is spread both by animal to animal contact and through the environment. Since its detection in Colorado in the late 1960s, CWD has continued to spread across North America and is now found in 18 U.S. states and 2 Canadian provinces (Conner & Miller 2004; Oyer *et al.* 2007; Skuldt *et al.* 2008). Disease surveillance data from hunter-harvested deer indicates differences in the emerging patterns of spatial spread of CWD in wild populations may be influenced by spatial heterogeneities in the landscape (Joly *et al.* 2006; Rees *et al.* 2012). For example, high CWD prevalence has been related to the amount of forest cover in Wisconsin (Joly *et al.* 2006), urban areas in Colorado (Farnsworth *et al.* 2005) and agricultural land adjacent to the river valleys in Saskatchewan

(Rees et al. 2012). These patterns may reflect high deer densities resulting in increased home range overlap and larger group sizes that alter contact rates particularly in areas of preferred habitat (Kjaer *et al.* 2008; Habib *et al.* 2011; Silbernagel *et al.* 2011). In Wisconsin and Illinois, the disease appears to be spreading outward from a core area of infection (Osnas *et al.* 2009; Shelton & McDonald 2011). In contrast, disease spread in Saskatchewan and Nebraska appears to be moving faster along the South Saskatchewan and Missouri River (Clements *et al.* 2011; Walter *et al.* 2011b; Rees *et al.* 2012). This suggests that landscape features play an important role in directing deer movements and CWD spread (Clements et al. 2011, Blanchong et al. 2008).

In this chapter, I assess the risk of CWD being found in deer harvested from areas in east-central Alberta. I used surveillance data collected from 2000 to 2010 in Saskatchewan (SK) and Alberta (AB) to derive a disease risk model (P_{IDM}) that predicts the probability of a harvested deer being CWD positive (CWD+) based on the species and sex of the deer, landscape features surrounding the area where a deer was harvested (kill site), and metrics of landscape connectivity to known disease sources. I included deer species and sex because prevalence has been shown to be highest in mule deer and males across geographic regions (Miller *et al.* 2000; Conner *et al.* 2007; Osnas *et al.* 2009). Habitats I hypothesized deer would prefer were measured around the kill site because preferred habitat may increase deer aggregation and thus transmission likelihood (Begon *et al.* 2002). I also compared Euclidian distance (proximity) and metrics of connectivity that integrated deer movement responses to landscape features using a step selection

function (SSF, Fortin *et al.* 2005) and circuit theory (McRae *et al.* 2008). I utilized a connectivity metric derived from animal movements to predict disease occurrence, but unlike earlier studies (Bar-David *et al.* 2006; Remais *et al.* 2010; Garlick *et al.* 2011), connectivity metrics were evaluated against a null hypothesis of Euclidean distance measured based on observed disease locations. Finally, I illustrated the application of the model to evaluate the relative risk of CWD being found in 7 currently “CWD-free” Wildlife Management Units (WMUs) adjacent to the core CWD infected area. My focus was on landscape connectivity and determining the importance of host movement for disease introduction into new areas.

Materials and Methods

STUDY AREA

The study area includes ~67,000 km² of rolling hills located near Wainwright, AB (52°50'10.31"N, 110°51'31.18"W) along the AB-SK border (Fig. 2.1). The area is largely within the aspen parkland ecosystem with small portions of boreal transition in the north and moist mixed-grasslands in the south (Bird 1961). The Battle River, North Saskatchewan River and Ribstone Creek are the major drainages with a few large lakes and numerous ponds and wetlands scattered throughout (4.7% of land cover). Land use is dominated by agriculture (67.5%) and anthropogenic features like oil and gas development (0.3 wells/km²) and roads (0.9 km/km²). Native land cover types include: deciduous forest (6.5%) primarily around rugged terrain like river valleys, coniferous and mixed forest

(0.5%) concentrated at the northern extent, shrublands (7.4%) and grasslands (12%, Agriculture and Agri-Food Canada 2010). Deciduous forest is dominated by trembling aspen *Populus tremuloides* Michx. and balsam poplar *Populus balsamifera* L. and coniferous forest by white spruce *Picea glauca* (Moench) Voss, black spruce *Picea mariana* (Mill.) B.S.P., and jackpine *Pinus banksiana* Lamb. Shrubs consist mainly of *Elaeagnus commutata* L., *Amelanchier alnifolia* Nutt., *Prunus* spp. and *Symphoricarpos* spp. with native grasslands dominated by plains rough fescue *Festuca halli* (Vasey) Piper (Acton et al. 1998).

Across the area, mule and white-tailed deer population densities were highly variable ranging up to 3.6 mule deer/km² and 2.6 white-tailed deer/km² in a wildlife management unit (Alberta Fish and Wildlife, unpublished data). As of 2010, 92 mule deer and 10 white-tailed deer CWD+ cases were detected within the study area. Elk (*Cervus canadensis* Erxleben) and moose (*Alces alces* L.) are also present as other possible CWD hosts, but the disease has been detected only in elk in areas in SK about 410 km outside the study area. Predators include primarily humans and coyotes (*Canis latrans* Say). In AB, the white-tailed deer harvest in this region since 2000 has been based on an open license except in two WMUs, where the harvest was on a limited draw. Mule deer harvest was based on a limited availability license from 2000 to 2008 when Alberta added an open antlerless license in 4 of the 13 WMUs occurring in the study area. In 2006, AB instituted an additional “quota harvest” for CWD infected WMUs and those at risk with licenses that allowed for the harvest of 3 deer of either species (2 antlerless and 1 antlered). In SK, from 2000 to 2010, white-tailed deer harvest

was on an open license while mule deer licenses were limited. However, in 2008 SK adopted the “earn a buck” program. The earn-a-buck program required hunters to harvest two antlerless deer and submit heads for CWD testing before receiving an additional antlered license (WMU 46 and 47). Earn a buck was expanded to WMU 26 and 45 in 2009 then retracted to only 45 in 2010.

MODELING CWD RISK IN HARVESTED DEER

Deer samples and disease testing. In SK, heads from hunter-harvested deer were submitted for disease testing on a voluntary basis, except in areas where the earn-a-buck program was enforced. In AB, head submissions from hunter-harvested deer were either mandatory or voluntary from 2005 to 2008 depending on the WMU, but became mandatory in all CWD units ($n = 13$) in 2009. Most hunter-harvested deer (>90%) were killed from November to December, with the remainder from September to October. Hunters provided harvest date and kill site as either the GPS location or legal land description as the center of a quarter-section or section with an assumed accuracy of 0.65 km^2 and 2.56 km^2 . Heads of deer harvested from a herd-reduction program (2006-2008) in AB were also submitted for CWD testing and included in this study. Collections of these deer occurred in February or March by sharpshooters on the ground (2006) and in helicopters (2007-2008) within a 10-km radius of previous CWD+ cases. In all cases, only deer samples with complete information were considered for analysis. Deer age was not determined for the AB hunter-harvested deer and as a result animal age was not included in this analysis.

In SK, deer > 9 months of age were tested at the Prairie Diagnostic Services using anti-TSE monoclonal antibody F99/97.6.1 (Veterinary Medical Research & Development Inc.) and a Ventana Benchmark automatic IHC stainer (Ventana Medical Systems Inc.) on the tonsils and retropharyngeal lymph nodes (Chiu *et al.* 2009). In AB CWD testing was done on all deer by Alberta Agriculture and Rural Development, which analyzed the retropharyngeal lymph nodes using a BioRad ELISA test (Gavier-Widen *et al.* 2005). Both provinces sent non-negative samples to the Canadian Food Inspection Agency Laboratory to confirm the result using BioRAD ELISA, PrP immunohistochemistry, and western immunoblot tests.

Of the surveillance data collected from 2000 to 2010, only the 2005-2010 data were used to estimate the P_{IDM} while 2000-2004 CWD+ cases were used as disease sources for calculating connectivity. Because of the large sample of deer harvested that tested CWD- (>19,000) and the associated processing time in developing connectivity metrics (see below), I used data in this analysis only from: (1) CWD- deer within 90 km from detected CWD+ deer from previous years, which reflected the maximum distance that a CWD+ deer was detected from CWD+ in previous years in this study (87 km this study), which was similar to southern SK where 90% of CWD+ were within 90 km of previous CWD+ (Rees *et al.* 2012), and (2) deer from a subset (25%) of the CWD- deer that were randomly and proportionally selected from each year. In contrast, I used all observations of CWD+ deer from 2005 through 2010 ($n = 94$).

Kill site characteristics. Covariates of kill sites were measured either within a circular buffer of varying sizes (3, 6 and 12 km²) or as the shortest distance to a

linear feature or source of disease (Table 2.1). The range of buffer sizes reflected the range in deer home range sizes in the study area across species and sex in winter (4.8 to 12.7 km²) and summer (4.5 to 6.4 km², E. Merrill, unpublished data). Proportions of agriculture and woody cover were calculated from a land-cover map derived with ETM+ multi-spectral imagery and Landsat 5 TM at a 30-m resolution (Agriculture and Agri-Food Canada 2010). Measures of terrain ruggedness were derived from a 30-m digital elevation model. Distance to well sites with an accuracy of ± 20 m was measured for active, abandoned and newly licensed oil and gas wells current as of 23 January 2006. Linear waterways like rivers and streams were identified from a single-line network layer developed from a digital elevation model. GIS base layers and environmental layers were provided by Spatial Data Warehouse Ltd., Agriculture and Agri-Food Canada and Saskatchewan Environment.

Proximity to disease sources were measured as either the straight-line distance to the (1) nearest (km) or (2) the average distance (km) to the kill location of all previously known CWD+ deer. Landscape connectivity metrics were calculated as resistance, which is the inverse of connectivity. Similar to proximity, metrics of landscape connectivity to previous CWD+ (see below) were calculated as: (1) the single most connected (lowest resistance) CWD+ case and (2) the mean connectivity to all CWD+ cases. All spatial analyses were done in ArcGIS 9.3.1 (ESRI, Redlands, CA, 2009).

Statistical analyses. I used the rare events logistic regression function (relogit) in R.2.3.1 (R Development Core Team 2011) within the package ZELIG (Imai *et al.*

2008; Imai *et al.* 2011) to model the probability (P_{IDM}) of a deer being CWD+ (1) or CWD- (0). I chose this approach because it corrects for bias in parameter estimation caused by a low number of samples in one binary category (i.e. CWD+, King & Zeng 2001). P_{IDM} takes the form:

$$Y(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)} \quad \text{eqn 2.1.}$$

where $x_1 \dots x_p$ include covariates for deer species, sex, harvest type (hunter; herd reduction), province (AB, SK), time (t) in years since first CWD detection (i.e. 2000), environmental characteristics of the kill site and either proximity or landscape connectivity metrics. β_0 is the regression constant and $\beta_1 \dots \beta_p$ are the coefficients estimated for the variables $x_1 \dots x_p$.

I included species, sex, and time in years since first detection (t) in the region (20 November 2000) because they are known to influence probability of an individual deer being infected (Heisey *et al.* 2010; Walsh & Miller 2010; Rees *et al.* 2012), as well as the province to account for differences in surveillance regime or disease history (Table 2.1). Harvest type was included because herd reductions were done in areas where positives had been previously detected, therefore may be more likely to harvest a positive compared to samples obtained from hunters collected throughout the study area. Values for t were assigned as integer values for hunter-harvested deer, but because herd reductions were in late winter (February or March) t values for herd reduction harvested deer were derived as the difference between the median date of the herd reduction event and 20 November 2000 in decimal years. All covariates were tested for correlation and

were not placed in the same model if they were strongly correlated based on Spearman's rank correlation ($r_s \geq 0.50$, $P < 0.05$). I used Akaike information criterion (AIC) to rank *a priori* competing models, and then model averaged those constituting the top > 95% AIC weight (Anderson 2008). I assessed P_{IDM} predictive ability using area under the receiver operating curve (AUC, Fielding & Bell 1997) in the package ROCR (Sing *et al.* 2005) in R.2.3.1. To determine covariate importance I calculated fully standardized logistic regression coefficients, which quantifies the number of standard deviations P_{IDM} will differ per one standard deviation covariate difference (Menard 2004).

LANDSCAPE CONNECTIVITY

I derived 6 metrics of connectivity between a kill site location and previously detected cases of CWD+ deer to determine whether connectivity based on deer movement predicted the probability of deer harvested on the landscape being CWD+ were better than metrics based on Euclidean distance alone. Connectivity metrics were derived by combining “resistance” values derived from a step selection function (SSF, McRae & Beier 2007; McRae *et al.* 2008) of GPS-collared deer with circuit theory using the program CIRCUITSCAPE (v.3.5, McRae *et al.* 2008). I chose this approach to calculating connectivity because the SSF reflects the willingness of deer to select a movement path and circuit theory evaluates all possible paths between locations rather than a single optimal path as in least cost path analysis (McRae & Beier 2007; Urban *et al.* 2009; Dale & Fortin 2010).

Deer movement. Movements of 20 GPS-collared mule deer (male = 8, female = 12) and 18 GPS-collared white-tailed deer (male = 5, female = 13) monitored from 2006 to 2008 were used to develop a SSF. Deer were captured using Clover traps (Clover 1954) baited with hay and oats or by helicopter net-gunning (Barrett *et al.* 1982). Adults were fitted with GPS-collars (Lotek 3300S/4400S; Lotek Wireless, Newmarket, Ontario, Canada; or HABIT GPS collars, HABIT Research Ltd., Victoria, BC, Canada). Collars deployed on males were modified by adding a section of elastic surgical tubing to accommodate neck-swelling during the rut. Capture and handling procedures were in accordance with animal care protocol and provincial permits (Univ. Alberta #4941001; Alberta Sustainable Resource Development RP: #39576, CL: 39504; Alberta Tourism, Parks, and Recreation #RC09EC003, RC09EC005; Saskatchewan Ministry of Environment #09FW028).

Deer movements were monitored at a 2-hr frequency. Average location error was 7.5 ± 8.4 m (SD) with a > 99% fix success rate (n = 1148) across all vegetation types during an 8-day trial with a stationary collar hung 1 m off the ground taking 1-hr fixes. To approximate selection during long range movements, only locations outside of winter (27 March to 24 December) were used, when dispersal and migration are most common (Nelson 1998; Nelson *et al.* 2004; Nixon *et al.* 2007; Nixon *et al.* 2008).

Step selection function. I used values predicted from SSF to build the resistance surfaces (Spear *et al.* 2010) for input into CIRCUITSCAPE. The SSF uses a case-control, conditional logistic design to compare characteristics of “steps” along a movement path to those which were available with steps represented by a straight

line connecting two consecutive GPS locations (Fortin *et al.* 2005). The SSF is a function of the probability of an animal choosing a step based on environmental covariates along the step. I made independent SSF models for mule deer (MUDE) and white-tailed deer (WTDE). Observed steps were matched with 15 available steps that shared an origin and were drawn stochastically from empirical step length (SL) and turn angle (TA) frequency distributions. SL and TA were drawn independently because there was minimal circular-linear correlation ($r < 0.02$ for all deer, Batschelet 1981). Equal numbers of observed steps per deer were used so that all individuals contributed evenly to the models (116 steps/mule deer and 198 steps/white-tailed deer). SL and TA of individual deer were pooled among deer of the same species and sex (e.g. MUDE female) within equal 50-m intervals up to 3000 m for the SL distribution and equal 24° intervals from -180 to 180° for the TA distribution. I further combined pooled distributions across species and sex when Kolmogorov-Smirnov tests (Zar 1999) were non-significant ($P > 0.05$), otherwise distributions remained separate.

I used conditional logistic regression in STATA[®] 10 (StataCorp 2007) to derive the SSF equation:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \beta_3 x_3 + \dots + \beta_\rho x_\rho) \quad \text{eqn 2.2.}$$

where $x_1 \dots x_\rho$ are landscape covariates and $\beta_1 \dots \beta_\rho$ are the parameters. Robust standard errors were calculated using the Sandwich variance estimation method based on individual deer using CLUSTER in STATA (Rogers 1993; Williams 2000). Landscape covariates included: terrain ruggedness ($\text{Rugg}_{175\text{m}}$, $\text{Rugg}_{300\text{m}}$),

terrain slope (Slope), distance to roads (Dpavgrav, Dhiway, Droad), distance to well sites (Dwell), tree and shrub cover (Cov_{175m}, Cov_{300m} & Dcov) and distance to water bodies and streams (Dwater & Dstream, Table 2.1). *A priori* competing models were ranked and a final model chosen using Akaike's information criterion for small sample size (AIC_c, Burnham & Anderson 2002). The top SSF models were tested for sex effects on model parameters but they were negligible (Appendix 1).

Connectivity metrics. To quantify landscape connectivity between two locations, I used the program CIRCUITSCAPE, which is based on a graph theoretic approach where edges connecting graph nodes are analogous to resistors in an electrical circuit allowing for application of circuit theory principles like Ohm's law (McRae 2006; McRae *et al.* 2008). The MUDE and WTDE SSF were incorporated into CIRCUITSCAPE by providing a resistance surface for the landscape, with inverse SSF values equating to resistance. Resistance surfaces were calculated initially at 30 x 30-m cell, and then smoothed to 1000 x 1000-m cell size by taking an inverse distance weighted mean of input cell values using bilinear interpolation (ESRI 2009). To reduce bias in connectivity values calculated near map edges, I buffered all rasters covering the extent of the study area by 50 km. Where GIS layers did not extend beyond the study area, the buffer was composed of random values drawn from within the study area (Koen *et al.* 2010). To measure connectivity based on both species, I chose not to construct a third SSF but instead combined the MUDE and WTDE SSF and weighted them by prevalence. The combined surface was built by reclassifying the MUDE and

WTDE resistance surfaces to integer values from 1 to 10 based on 10 quantile bins, to make the two SSF model values relative to each other. Then adding the resulting surfaces together, but weighting the MUDE SSF surface by 7x to account for higher CWD prevalence in mule deer (this study). I weighted by prevalence based on the assumption that mule deer movements have a greater impact of CWD spread than white-tailed deer proportional to their higher prevalence.

ASSESSING CWD RISK IN “DISEASE-FREE” WMUs

I assessed the risk of CWD being detected in deer harvested in 7 currently “CWD-free” WMUs in AB (Fig. 2.1) based on the P_{IDM} and known composition of deer in these areas. First, I used the P_{IDM} to create 4 spatial risk maps (30 x 30-m pixels) of predicted P_{IDM} values for mule deer and white-tailed deer of both sexes, and aggregated values to a cell size of 100 x 100-m using inverse distance weighted mean of input cell values with bilinear interpolation (ESRI 2009). Second, using information on deer species and sex composition (see below), I derived a population-adjusted measure of risk of CWD as:

$$RISK = \sum D_{ij} P_{IDMij} \quad \text{eqn 2.3.}$$

where D_{ij} is the probability that a randomly chosen deer in a WMU is of species i (mule deer, white-tailed deer) and sex j (male, female) and P_{IDMij} is the probability that a harvested deer of species i and sex j from a pixel in year 2011 is CWD+ given the landscape characteristics of the cell with a possible range of values from zero to one. In this example, D_{ij} was based on 2011 pre-hunting

season deer population in a WMU based on winter aerial survey data extrapolated across years with a population model (Appendix 2). Aerial surveys were based on stratified random sampling with 20% coverage (Alberta Fish and Wildlife, unpublished data). No corrections were made for deer sightability bias, but detection of deer in these habitats was $> 90\%$ when snow was present (Habib et al. in press).

Results

STEP SELECTION FUNCTIONS AND RESISTANCE SURFACES

Because there was no difference in turn angle between species ($P=0.80$) or sex ($P=0.17$), I combined data on TA for all deer (Appendix 3). In contrast, I found differences in step length distributions between species ($P<0.01$) and sex in white-tailed deer ($P<0.01$) but not mule deer ($P=0.10$), based on Kolmogorov-Smirnov tests. Therefore, I used one TA distribution and three SL distributions to determine random paths of deer for the two species to compare to used paths in the step selection function.

The top SSF for mule deer ($w_i = 0.74$) and white-tailed deer ($w_i = 0.99$) had similar environmental influences with distance to cover, distance to water and a measure of terrain ruggedness included in both SSFs, although the scales of measurement differed (Table 2.2). Both species selected to move near cover and far from water, but mule deer selected to move in areas of terrain ruggedness, while white-tailed deer moved in gentle terrain (Table 2.3). White-tailed deer

preferred gentle terrain especially when distant from water (Fig. 2.2). No covariates in the top models were strongly correlated ($r < 0.6$, Appendix 4).

P_{IDM} MODEL

CWD surveillance data were collected from 2471 mule deer and 751 white-tailed deer harvested during hunting seasons from 2000-2010 in SK and 9444 mule deer and 6886 white-tailed deer were harvested in AB from 2006 to 2010 (Table 2.4). Of the deer harvested from AB, 15% of the mule deer and 38% of the white-tailed deer were harvested during the herd reduction program. In SK, prevalence showed a linear increase of 1.7x/year between 2005 and 2010, while in AB the increase was 1.2x/year between 2006 and 2010 (Fig. 2.3). Within the study area in 2010, SK mule deer prevalence was 0.03 ($n = 297$) with no CWD+ detected among sampled white-tailed deer ($n = 20$), while in AB prevalence was 0.007 ($n = 1710$) and 0.002 ($n = 844$) in mule deer and white-tailed deer respectively (Table 2.4). In the P_{IDM} base model I included deer species, sex, t , province and type of harvest because of their significant P -values (Table 2.5) and removing any of these covariates increased the $\Delta AIC \geq 10$ (Appendix 5).

Beyond the base model, the top P_{IDM} included 4 environmental covariates, mean connectivity based on the MUDE SSF ($M_{Resistance}$) and 5 covariate interactions (Table 2.6). According to the AIC rankings, there was support for adding these landscape covariates and their interactions to the base model. Only two alternative models had equal weight of evidence as the top model, and these models differed by omitting only a single interaction term that reflected

differences in either distance to roads or stream density between provinces. For the final P_{IDM} , I model averaged the top three models and the averaged model had an AUC score of 0.85.

According to the odds ratios (e^{β}) from the P_{IDM} (Table 2.5), deer harvested during herd reductions had a 15.5x higher odds of being CWD+ than those harvested by hunters. Throughout the study area, CWD risk increased by 1.5x from year to year. The odds of a mule deer being infected were 4.8x higher than a white-tailed deer. A male's odds of being CWD+ were 0.9x as likely than females according to the sex coefficient alone; however, when accounting for the interaction with ruggedness fixed at its median value (Appendix 6), males had 1.7x higher risk than females. The odds ratio of a deer being CWD+ increased when it was harvested in an area of high agricultural extent, gentle terrain, with high stream density, close to roads and well connected to areas where CWD+ deer were previously harvested. Deer harvested in the herd reduction program were less likely to be infected in areas of high terrain ruggedness, but ruggedness had little effect on hunter-harvested deer (Fig. 2.4). Deer harvested near roads (human-dominated areas) in agricultural areas were more likely to be CWD+ than when they were harvested far from roads in agricultural areas (Fig. 2.5).

CONNECTIVITY AND PROXIMITY

The proximity or connectivity metric with the greatest support for inclusion in the P_{IDM} was $M_{Resistance}$ or mean connectivity based on the MUDE SSF. If $M_{Resistance}$ was replaced in the top P_{IDM} by WTDE SSF, DEER SSF or proximity

then AIC_c increased significantly by 10.7, 8.6 or 19.8 respectively. But regardless of which proximity or connectivity metric was included in the P_{IDM} , locations farther from or less connected to known sources of CWD+ deer had reduced CWD risk.

ASSESSING CWD RISK

The ratio of mule deer to white-tailed deer within the deer population in the 7 WMUs ranged between 0.13 and 1.98. WMUs with a high proportion of mule deer (i.e., WMU 730 and 203) had mean RISK values 1.2 to 2.2x that of the other WMUs (Table 2.7). Artificially varying herd composition influenced the rankings of mean RISK in each WMU (Fig. 2.6). While varying herd composition increased or decreased RISK, it had little effect on the underlying spatial pattern of RISK (Fig. 2.7) because herd information was input only at the scale of the WMU. In contrast, spatial patterns in RISK within a WMU emerged largely due to connectivity (Fig. 2.8) with fine-scale variation due to other landscape features emerging when connectivity was high (Fig. 2.9). In particular, the importance of connectivity was demonstrated in the northern WMUs of 258 and 500 wherein connectivity is high despite being distant from the majority of previous CWD+ cases (Fig. 2.10) making predicted CWD risk for the proximity based P_{IDM} much lower compared to the connectivity P_{IDM} (Fig. 2.11). I also included a quadratic term for proportion of agriculture in the proximity P_{IDM} , in an attempt to replicate the pattern of the connectivity P_{IDM} by allowing risk to increase initially with agriculture, but then decrease for areas of high agriculture. However, the risk pattern still differed from the connectivity based P_{IDM} (Fig. 2.11).

Discussion

My results support that more realism and recognition of landscape connectivity is needed in studies of disease spread (Remais *et al.* 2010). Euclidian distance alone had less support for modeling disease risk because it ignored landscape heterogeneity. To my knowledge, I am the first to show a direct link between the occurrence of disease and empirically derived connectivity measures reflecting host movements in a heterogeneous landscape. These results have been inferred from previous studies that linked genetic relatedness to disease occurrence (Archie *et al.* 2009; Biek & Real 2010). For example, patterns in relatedness have indicated that the spread of raccoon rabies in the eastern United States and Canada may be impeded by major rivers (Rees *et al.* 2008), but not by ridge tops dividing adjacent valleys (Root *et al.* 2009). However, where data on movements are available, movement-based metrics of connectivity may better inform models predicting disease spread than genetic studies. For example, genetics of mule and white-tailed deer in this area showed little spatial structure beyond 2 km with the only identifiable large-scale barrier being the Canadian Rocky Mountains (Cullingham *et al.* 2011a; Cullingham *et al.* 2011b). They attributed this to the high mobility of deer (Nelson 1993; Long *et al.* 2005) and recent expansion of white-tailed deer populations (Wishart 1984) with insufficient time to establish a stable genetic structure (Austerlitz *et al.* 1997; Hutchison & Templeton 1999). Cullingham *et al.* (2011a) were able to show greater relatedness among infected female mule deer at the small scale (< 2 km) suggesting that transmission within groups of related philopatric females (Bowyer 1984; Lingle

2003) is important to CWD spread. Except for the Rocky Mountains, they could suggest only distance as a limiting factor via dispersal and migration can explain large scale spread between groups or populations (Conner & Miller 2004; Oyer *et al.* 2007; Blanchong *et al.* 2008).

In contrast, I found deer movements were influenced by landscape features, based on their incorporation into the CWD risk model, indicating that movement may reflect processes of disease spread better than distance or genetic relatedness. Because local factors within the P_{IDM} were expected to control fine-scale influences on the disease spread (i.e. deer-deer contact rates, Habib *et al.* 2011), I interpret the connectivity metrics to reflect the spread of CWD driven by movement of infected deer into new areas as they establish the initial disease spark (Oyer *et al.* 2007; Jackson *et al.* 2008). This is despite the fact that the data I used to quantify connectivity were based on non-dispersal movements due to the difficulty of observing dispersal (Clobert *et al.* 2009; Spear *et al.* 2010). Using non-dispersal movement to reflect where animals may travel is a common approach (Chetkiewicz & Boyce 2009; La Morgia *et al.* 2011) that has support from genetic studies. Cushman & Lewis (2010) used the same approach for modeling landscape connectivity of black bears with a relationship between connectivity and individual genetic relatedness of bears. A preliminary comparison of habitat selection, for the same GPS collared deer in this study, for movements inside versus outside their 90% kernel UD home range found no major differences in selection (E. Merrill, unpublished data). As a result, I analyzed all movements to capture deer responses to a broad range of habitat

conditions. However, if dispersers tend to move more in straight-line paths resulting in lower selectivity (Palomares *et al.* 2000; Selonen & Hanski 2006), then proximity should have had as much support as connectivity, but this was not the case.

In the open environments of the Prairie parklands, mule and white-tailed deer preferred to travel through or close to aspen or shrub cover probably because it is important for security cover (Nixon *et al.* 1991; Foster *et al.* 1997; Grovenburg *et al.* 2011) for reducing predation risk (Festa-Bianchet 1988; Bowyer *et al.* 1999; Fortin *et al.* 2005; Fischhoff *et al.* 2007). Both deer species moved farther away from ponds, lakes and rivers to avoid crossing these features (Eberhardt *et al.* 1984; Lang & Blanchong 2012) despite both species being able to swim (Robinett 1966; Inglis *et al.* 1979). In contrast, the two species had different preferences for rugged terrain. White-tailed deer moved across less rugged terrain, whereas mule deer, which use a stotting gait ideal for hill climbing (Lingle 1992; Lingle 1993), rely upon rugged terrain to escape predators (Lingle & Pellis 2002; Lingle 2002). Despite this difference in movement preference and connectivity between the species when relating landscape connectivity to disease prevalence only the connectivity metric based on mule deer movements predicted CWD occurrence because there were few infected white-tailed deer (10%) compared to mule deer (90%). For mule deer, the river drainages appear to be important movement corridors, because rivers are a linear arrangement of rugged terrain and contiguous forest cover within an agricultural matrix (i.e. Battle River or Ribstone Creek). However, where rugged terrain and forest cover is not

exclusive to the river valleys (i.e. The North Saskatchewan River) disease spread is more diffuse as deer are less restricted in their movements, traveling not only along the rivers but across the landscape in all directions. This appears to be the case in the northern portion of the study area (Fig. 2.8). However, landscape connectivity and associated deer movement are not the only factor controlling spread. There are also local landscape factors that promote transmission between individuals (Begon *et al.* 2002; Greer & Collins 2008; Vander Wal *et al.* 2012).

For continued CWD spread, the infection must be able to effectively transmit between deer, with the landscape influencing transmission via deer densities, congregation and contact rates (Miller & Williams 2003; Miller *et al.* 2006). For example, agricultural areas immediately adjacent to river drainages had high predicted disease risk not only because they are well connected, but because they are quality mule deer habitat resulting in high local densities (E. Merrill, unpublished data). The river valleys are ideal mule deer habitat because of the steep terrain for escaping predators (Lingle 2002), abundant cover for bedding between feeding bouts (Silbernagel *et al.* 2011) and access to adjacent croplands with high quality forage (Nixon *et al.* 1991). The resulting high densities increase deer group sizes and deer contact rates (Lingle 2003; Habib *et al.* 2011), while the lack of forest cover associated with agriculture results in deer congregating within the remaining patches (Kjaer *et al.* 2008; Habib *et al.* 2011; Silbernagel *et al.* 2011), increasing the likelihood of transmission. While local landscape effects in the current model provide a good prediction of disease occurrence, subsequent models may be improved by including soil characteristics

(i.e. clay content) that are likely to influence indirect CWD transmission (Saunders *et al.* 2012a) by modifying the infectivity or longevity of soil bound prions (Saunders *et al.* 2011; Smith *et al.* 2011). For example, among free ranging mule deer in Colorado, increased soil clay content of an individual's presumed home range was correlated with the odds of deer being CWD infected (Walter *et al.* 2011a). I did not consider soil characteristics, because where disease occurrence was predicted I assumed there had been insufficient time to build up an environmental prion reservoir (Almberg *et al.* 2011), as no CWD+ had been detected at the time.

A stated goal for CWD management in Canada is to contain the disease to its current distribution, assuming eradication is not possible, by not allowing spread into new regions (Canadian Cooperative Wildlife Health Centre 2011). The risk model I have provided can help managers to achieve this goal by identifying areas where the disease is likely to spread based on landscape attributes and connectivity to previous known CWD cases. Then in these high risk areas managers can apply control efforts like targeted herd reductions. If hunting is the only disease control option, then managers should prioritize increasing mule deer and male harvest because of their higher prevalence. Although my results are specific to east-central Alberta, my overall approach to modeling risk can be applied to other CWD infected areas with sufficient surveillance data and ideally GPS collar data required for quantifying landscape connectivity. However, even if GPS collar data are lacking the effects of landscape on connectivity and deer movement could be approximated using the plethora of deer movement (Long *et*

al. 2010; Silbernagel 2010; Clements *et al.* 2011; Garlick *et al.* 2011) and habitat selection studies (Bowyer 1986; Pauley *et al.* 1993; Pierce *et al.* 2004; Sawyer *et al.* 2006; Sawyer *et al.* 2009; Anderson *et al.* 2012).

Table 2.1. Covariates used in either the step selection function analysis (SSF) or a model for predicting the probability of an individual deer harvested by hunters or in a herd reduction program between 2006-2010 being CWD+ analysis (P_{IDM}).

Covariate	Description	Analysis
Driver	Distance (m) to nearest major drainage including the Battle River, Ribstone Creek and North Saskatchewan River	P_{IDM}
Dstream	Distance (m) to nearest river or stream.	P_{IDM} , SSF
Dms	Distance (m) to nearest minor stream not part of the major drainages (Battle, Ribstone and North Saskatchewan).	P_{IDM}
Stream _{3km} , Stream _{6km} & Stream _{12km}	Length (m) of rivers and creeks within a 3, 6 and 12 km ² circular buffer.	P_{IDM}
Dwater	Distance (m) to nearest lake, pond, river or stream.	SSF
Droad	Distance (m) to nearest road includes paved, graveled and resource roads.	SSF
Dhiway	Distance (m) to nearest paved road.	SSF
Dpavgrav	Distance (m) to nearest paved or graveled road.	SSF
Road _{3km} , Road _{6km} & Road _{12km}	Length (m) of all roads in 3, 6 and 12 km ² circular buffer.	P_{IDM}
Dtown	Distance (m) to nearest city, town, village or hamlet.	P_{IDM}
Dwell	Distance (m) to nearest well site.	SSF
Dcov	Distance (m) to nearest woody cover (deciduous, coniferous and mixed wood forest or shrubs).	SSF
COV _{175m} , COV _{300m} , COV _{3km} , COV _{6km} & COV _{12km}	Proportion of woody cover (trees and shrubs) within a circular buffer with radius 175 or 300 m or with an area of 3, 6 and 12 km ² .	P_{IDM} , SSF
Agri _{3km} , Agri _{6km} & Agri _{12km}	Proportion of Agriculture (perennial, pasture and annual cropland) within a 3, 6 and 12 km ² a 3, 6 and 12 km ² circular buffer.	P_{IDM}
Open _{3km} , Open _{6km} & Open _{12km}	Proportion of natural grassland and agriculture within a 3, 6 and 12 km ² circular buffer.	P_{IDM}
Grass _{3km} , Grass _{6km} & Grass _{12km}	Proportion of natural grassland within a 3, 6 and 12 km ² circular buffer.	P_{IDM}

Table 2.1. Continued

Covariate	Description	Analysis
Rugg _{175m} , Rugg _{300m} , Rugg _{3km} , Rugg _{6km} & Rugg _{12km}	Standard deviation in elevation (m) within a circular buffer with radius 175 or 300 m or with an area of 3, 6 and 12 km ² .	P _{IDM} , SSF
Slope	Slope (%) for an individual cell.	SSF
M _{Resistance}	Average resistance (inverse of connectivity) to previous CWD cases based on mule deer SSF	P _{IDM}
Province	Province deer was harvested in: Alberta (1) or Saskatchewan (0)	P _{IDM}
Harvest	Harvest method: hunter (1) or cull (0)	P _{IDM}
<i>t</i>	Time in years since first CWD+ detected in 2000	P _{IDM}
Species	Deer species: Mule (1) or white-tailed deer (0)	P _{IDM}
Sex	Deer sex: male (1) or female (0)	P _{IDM}

Table 2.2. The five highest ranked step selection function models for mule deer and white-tailed deer in east-central Alberta and west-central Saskatchewan. Models were derived using 2-hour relocations on 20 GPS-collared mule deer (8 males; 12 females) and 18 GPS-collared white-tailed deer (5 males; 13 females) between 2006-2008 in east-central Alberta and west-central Saskatchewan. Presented are number of model parameters (k), Akaike's information criterion difference corrected for small sample size (AIC_c) and AIC_c weight (w_i). Covariate descriptions are provided in Table 2.1.

Species	Covariates	k	AIC_c	ΔAIC_c	w_i
Mule deer	Dcov, Rugg _{175m} , Dwater	4	12828.6	0.0	0.74
	Dcov, Rugg _{175m} , Dhiway, Dwater, Dwell	6	12831.7	3.1	0.16
	Dcov, Rugg _{175m}	3	12834.2	5.6	0.05
	Dcov, Dwater	2	12835.5	6.9	0.02
	Dcov, Dhiway, Dwater	4	12835.7	7.1	0.02
White-tailed deer	Dcov, Rugg _{300m} , Dwater, Rugg _{300m} x Dwater	5	19600.4	0.0	0.99
	Dcov, Rugg _{300m} , Dwater	4	19610.6	10.2	0.01
	Dcov, Rugg _{300m} , Droads, Dwater, Dwell	6	19617.3	16.9	<0.01
	Dcov, Dwater	3	19619.5	19.1	<0.01
	Dcov, Droad, Dwater	4	19621.3	20.9	<0.01

Table 2.3. Coefficients of the top step selection functions derived using 2-hr GPS relocations collected on 20 GPS-collar mule deer (8 males; 12 females) and 18 GPS-collared white-tailed deer (5 males; 13 females) between 2006-2008 in east-central Alberta and west-central Saskatchewan. Standard errors (SE) were adjusted using sandwich variance estimator by individual deer (Rogers 1993). Covariate descriptions are provided in Table 2.1.

Species	Covariates	<i>B</i>	SE	<i>z</i>	<i>P</i> -value
Mule deer	Dcov	-0.0028	0.0009	-4.97	< 0.01
	Rugg _{175m}	0.0556	0.0205	3.17	< 0.01
	Dwater	0.0007	0.0004	2.95	0.08
White-tailed deer	Dcov	-0.0074	0.0009	-7.66	< 0.01
	Rugg _{300m}	-0.0049	0.0270	-0.18	0.86
	Dwater	0.0014	0.0004	3.53	< 0.01
	Rugg _{300m} x Dwater	-0.0001	6.3E-05	-2.15	0.03

Table 2.4. Number of CWD positive (+) and negative (-) mule deer or white-tailed deer removed from the population by hunter-harvest or herd reduction from 2000 to 2010 in east-central Alberta and west-central Saskatchewan, Canada.

Year	Method	Alberta								Saskatchewan								
		White-tailed deer				Mule deer				White-tailed deer				Mule deer				
		Male		Female		Male		Female		Male		Female		Male		Female		
		+	-	+	-	+	-	+	-	+	-	+	-	+	-	+	-	
2000*	Hunter	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2001*	Hunter	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2002*	Hunter	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
2003*	Hunter	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
2004*	Hunter	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	0
2005	Hunter	0	0	0	0	0	0	0	0	0	23	0	90	1	70	1	261	0
2006	Cull	0	5	0	8	0	8	0	19	0	0	0	0	0	0	0	0	0
	Hunter	0	247	0	242	1	293	2	426	0	53	0	140	3	122	1	209	0
2007	Cull	1	246	0	554	2	225	6	366	0	0	0	0	0	0	0	0	0
	Hunter	1	566	0	438	2	772	1	1273	0	154	2	185	1	229	5	305	0
2008	Cull	0	500	2	1312	3	315	2	444	0	0	0	0	0	0	0	0	0
	Hunter	0	465	0	367	3	760	1	929	0	32	0	26	5	37	8	442	0
2009	Hunter	1	696	0	391	6	791	2	1082	0	20	0	5	1	20	6	440	0
2010	Hunter	2	525	0	317	9	845	3	853	0	9	0	11	2	11	8	276	0
	Total	5	3250	2	3629	26	4009	17	5392	0	291	3	457	18	489	31	1933	0

*Data from these years were used to calculate connectivity to previous positives but not to construct the P_{IDM} .

Table 2.5. P_{IDM} model parameters for predicting the probability that a harvest deer in 2005-2010 in east-central Alberta and west-central Saskatchewan is CWD+. Parameter values (B), standard errors (SE), confidence intervals (CI) and standardized regression coefficients (SRC). Covariate descriptions are provided in Table 2.1. For the species covariate mule deer is denoted by MUDE.

Covariate	B	SE	CI	SRC
Null model:				
Intercept	-7.05	0.70	-8.42, -5.67	-
Province (AB = 1)	-1.91	0.26	-2.42, -1.40	-0.21
Harvest (hunter = 1)	-1.33	0.35	-2.02, -0.65	-0.16
Time	0.31	0.09	0.15, 0.48	0.12
Species (MUDE = 1)	1.67	0.36	0.96, 2.39	0.24
Sex (male = 1)	0.79	0.23	0.34, 1.24	0.12
Full model:				
Intercept	-5.21	0.93	-7.03, -3.39	-
Agri _{12km}	2.29	0.63	1.04, 3.53	0.000036
Rugg _{12km}	-0.21	0.08	-0.37, -0.06	-0.000082
Droad	0.000557	0.000267	0.00003, 0.00108	0.000015
Stream _{3km}	0.000046	0.000116	-0.00018, 0.00027	0.000005
$M_{Resistance}$	-1.16	0.46	-2.06, -0.27	-0.440000
Province (AB = 1)	-1.39	0.44	-2.25, -0.54	-0.000026
Harvest (hunter = 1)	-2.74	0.65	-4.01, -1.47	-0.000055
Time	0.38	0.09	0.20, 0.56	0.000025
Species (MUDE = 1)	1.58	0.37	0.85, 2.30	0.000038
Sex (male = 1)	-0.09	0.38	-0.84, 0.65	-0.000002
Rugg _{12km} x Sex	0.06	0.03	0.01, 0.11	0.000023
Agri _{12km} x Droad	-0.00252	0.008	-0.00412, -0.00093	-0.000034
Rugg _{12km} x Harvest	0.18	0.08	0.02, 0.33	0.000077
Stream _{3km} x Province	0.000207	0.000114	-0.000017, 0.000431	0.000020
Droad x Province	-0.000751	0.000402	-0.00154, 0.000037	-0.000020

Table 2.6. Top P_{IDM} models predicting the probability that a harvested deer in 2005-2010 in east-central Alberta and west-central Saskatchewan is CWD+. Included are the number of estimated parameters (k) and AIC weight (w_i) for each model. Covariate descriptions are provided in Table 2.1.

P_{IDM}	Covariates	k	AIC	ΔAIC	w_i
1	Agri _{12km} , Rugg _{12km} , Droad, Stream _{3km} , M _{Resistance} , Province, Harvest, Time, Species, Sex, Agri _{12km} x Droad, Rugg _{12km} x Sex, Rugg _{12km} x Harvest, Stream _{3km} x Province, Droad x Province	16	779.0	0.0	0.61
2	1 – Droad x Province	15	781.2	2.2	0.20
3	1 - Stream _{3km} x Province	15	781.3	2.3	0.19
4	Agri _{12km} , Rugg _{12km} , Droad, Stream _{3km} , M _{Resistance} , Province, Harvest, Time, Species, Sex	11	807.3	28.3	<0.01
5	Province, Harvest, Time, Species, Sex	7	818.1	39.1	<0.01

Table 2.7. The mean (\bar{x}) and standard deviation (SD) of the RISK of a deer harvested within 100-m pixel being CWD+ as predicted by P_{IDM} and weighted by the herd composition (MM = mule deer males, MF = mule deer females, WM = white-tailed deer males, WF = white-tailed deer females) in each wildlife management unit (WMU). Covariate descriptions are provided in Table 2.1.

WMU	RISK		$M_{Resistance}$		Stream _{3km}		Agri _{12km}		Droad		Rugg _{12km}		Herd comp
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	MM/MF/ WM/WF
203	0.0067	0.0099	348.3	4899.7	2423.8	2444.7	0.82	0.17	389.7	328.6	9.7	8.1	0.20/0.47/ 0.08/0.25
238	0.0031	0.0042	5.6	17.6	1000.3	1641.2	0.88	0.12	344.1	280.6	9.4	6.3	0.08/0.19/ 0.18/0.55
730	0.0063	0.0037	1.2	0.1	546.8	1227.1	0.19	0.22	327.0	276.4	7.1	3.0	0.17/0.39/ 0.11/0.33
258	0.0051	0.0040	1.7	0.3	1929.7	1776.7	0.67	0.20	384.4	312.6	13.7	9.4	0.04/0.10/ 0.22/0.64
500	0.0033	0.0025	1.5	0.5	2136.3	1756.6	0.27	0.23	626.2	649.3	14.2	9.5	0.03/0.08/ 0.22/0.67
232	0.0053	0.0059	272.3	2855.8	1343	2134.0	0.85	0.12	369.1	296.5	10.0	6.4	0.15/0.34/ 0.13/0.38
254	0.0054	0.0051	246.1	3895.9	1765.9	1901.6	0.81	0.13	327.6	243.3	11.2	5.5	0.09/0.22/ 0.17/0.52

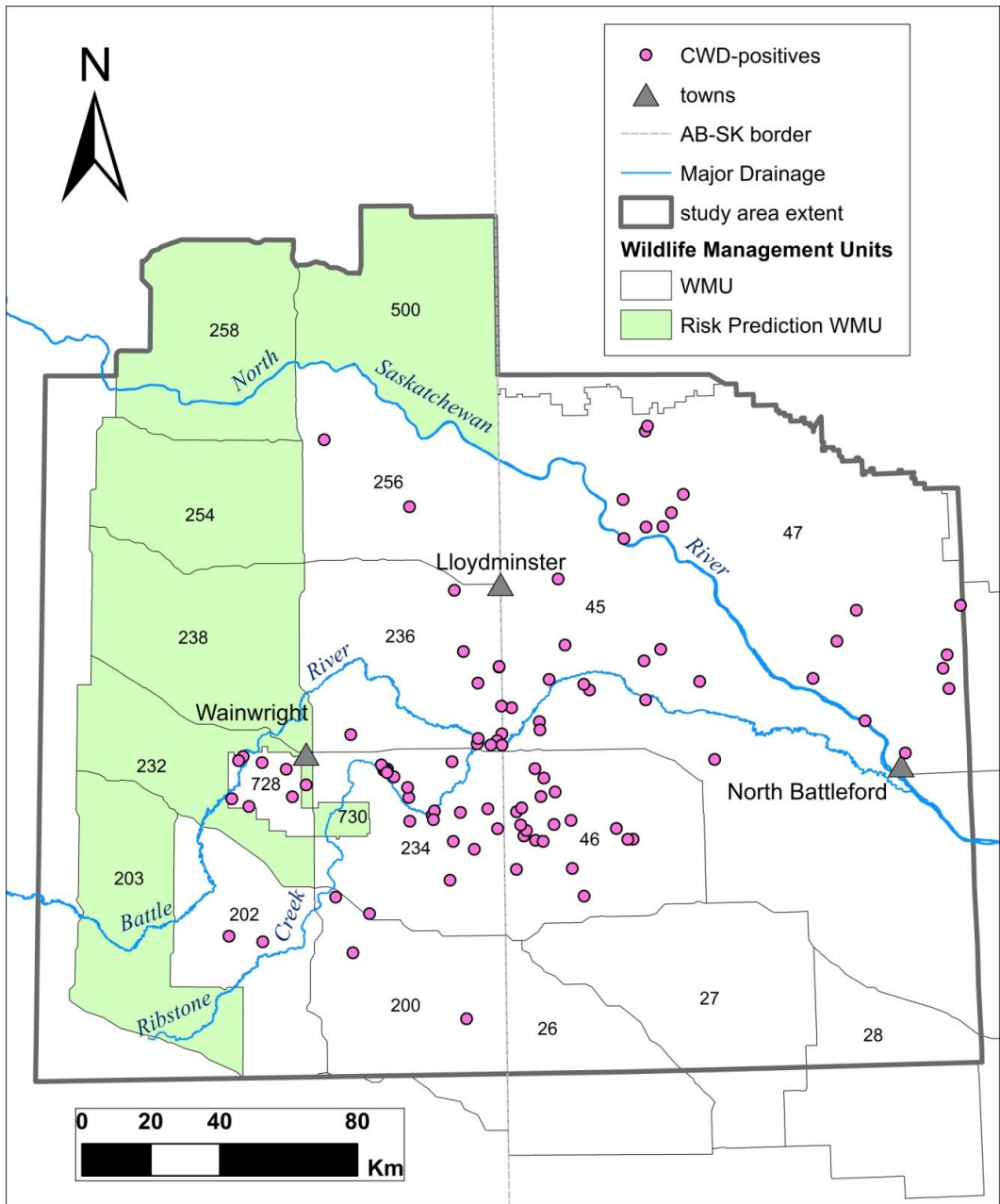


Fig. 2.1. Location of CWD positives detected from 2000 to 2010 in east-central Alberta and west-central Saskatchewan, Canada. CWD risk was predicted in the western and northern wildlife management units (WMU).

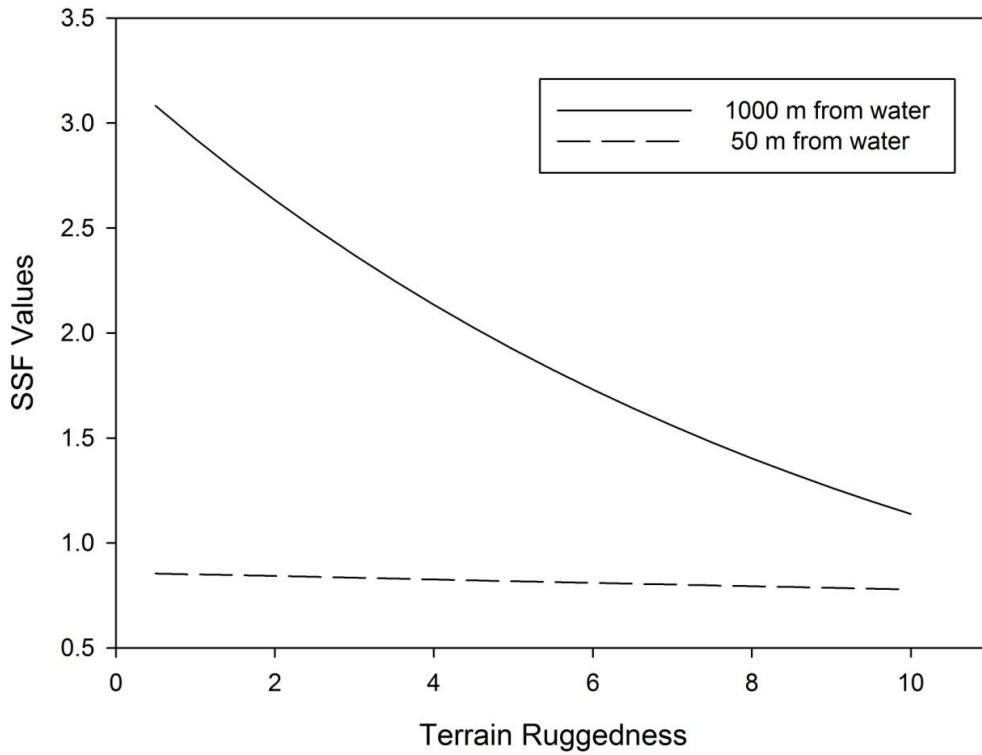


Fig. 2.2. Predicted white-tailed deer step selection function (SSF) values as a function of terrain ruggedness within a 300-m buffer ($Rugg_{300m}$) when a deer is 1000 m versus 50 m from a water body. The remaining covariate, distance to cover, is fixed at 30 m.

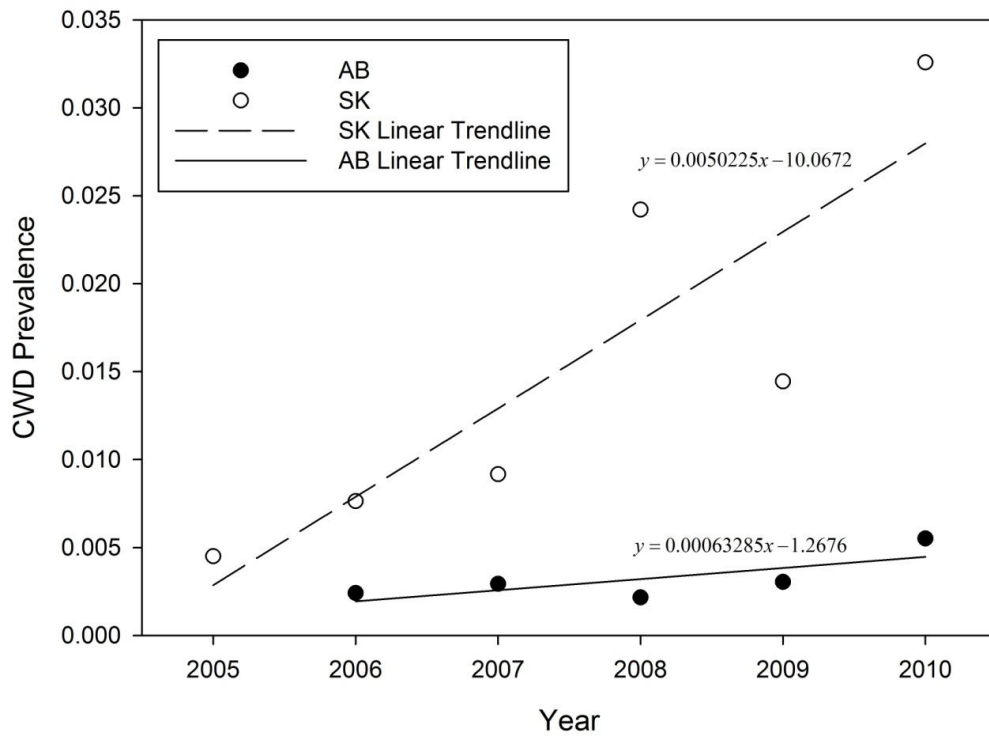


Fig. 2.3. CWD Prevalence from 2006 to 2010 in east-central Alberta (AB) and 2005 to 2010 in west-central Saskatchewan (SK) within the study area (not province wide) based on the hunter-harvest and herd reductions in AB and hunter-harvest only in SK. Prevalence is combined for mule deer and white-tailed deer of both sexes.

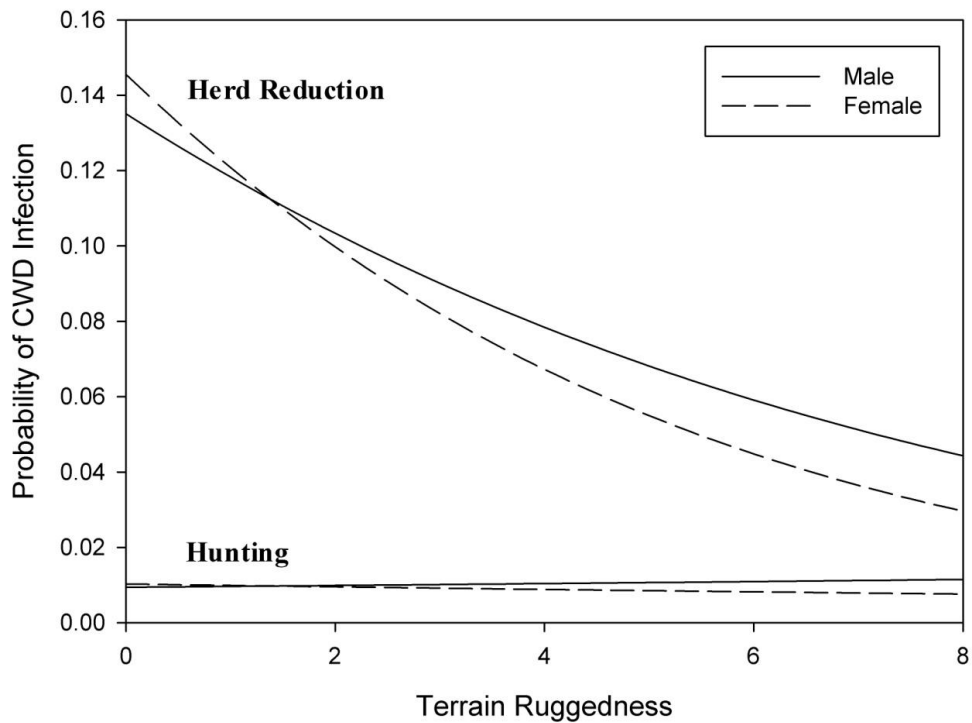


Fig. 2.4. Probability of a deer being CWD+ according to the P_{IDM} risk model as a function of terrain ruggedness within a 12-km² buffer ($Rugg_{12km}$) for male and female mule deer harvested by hunting or during the Alberta herd reduction program. Other continuous covariates within the P_{IDM} are set at their respective median values, province as Alberta and year as 2010.

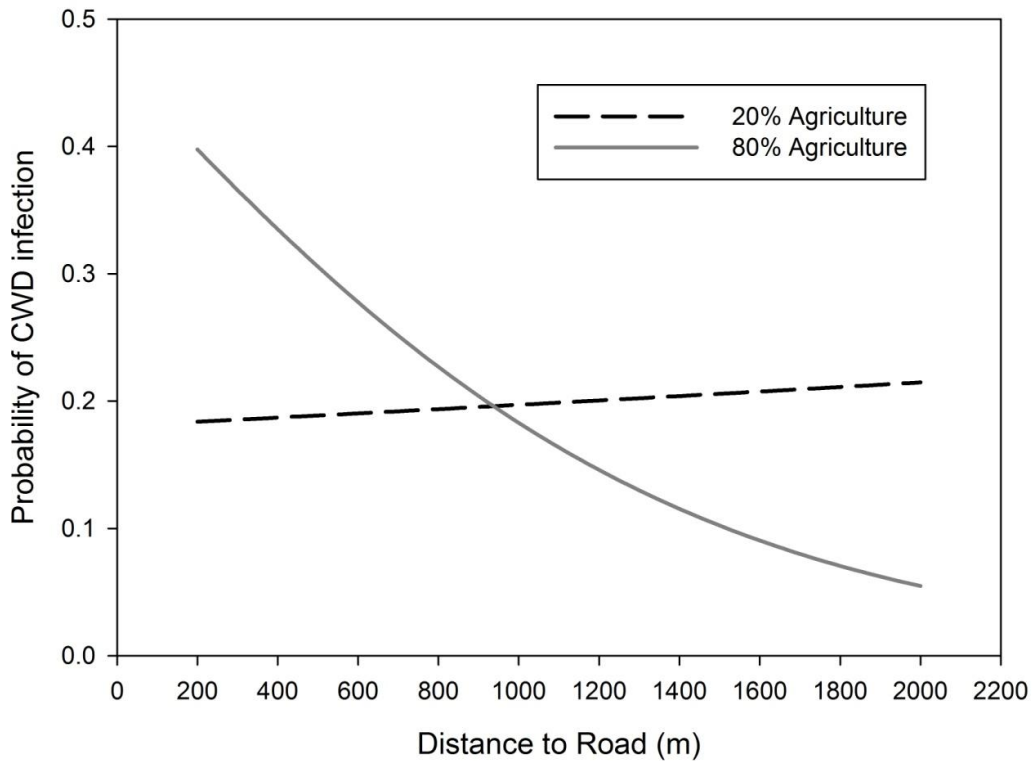


Fig. 2.5. Probability of a deer being CWD+ according to the P_{IDM} risk model as a function of proportion of agriculture land cover within a 12-km² buffer ($Agri_{12km}$) and distance to Road (Droad). Other continuous covariates set at respective median values and species as mule deer, sex as male province as Alberta and year as 2010.

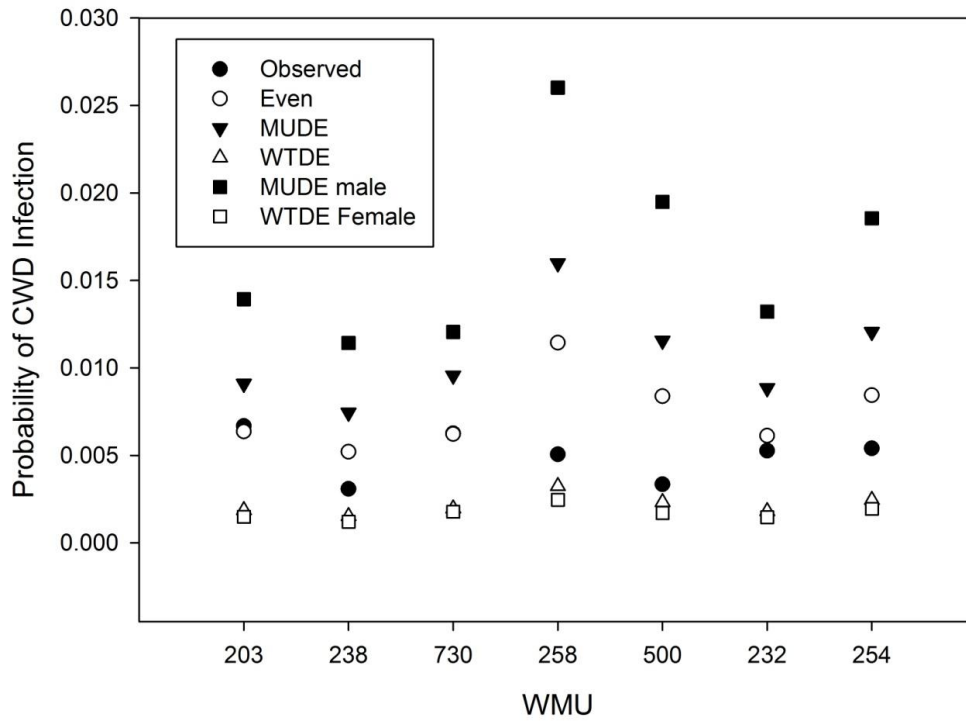


Fig. 2.6. Mean CWD risk for 7 Alberta WMUs derived from prediction of P_{IDM} at 100-m resolution and weighted by species and sex compositions including: observed composition, even species and sex, all mule deer (MUDE), all white-tailed deer (WTDE), mule deer males and mule deer females. The year in the P_{IDM} is set to 2011.

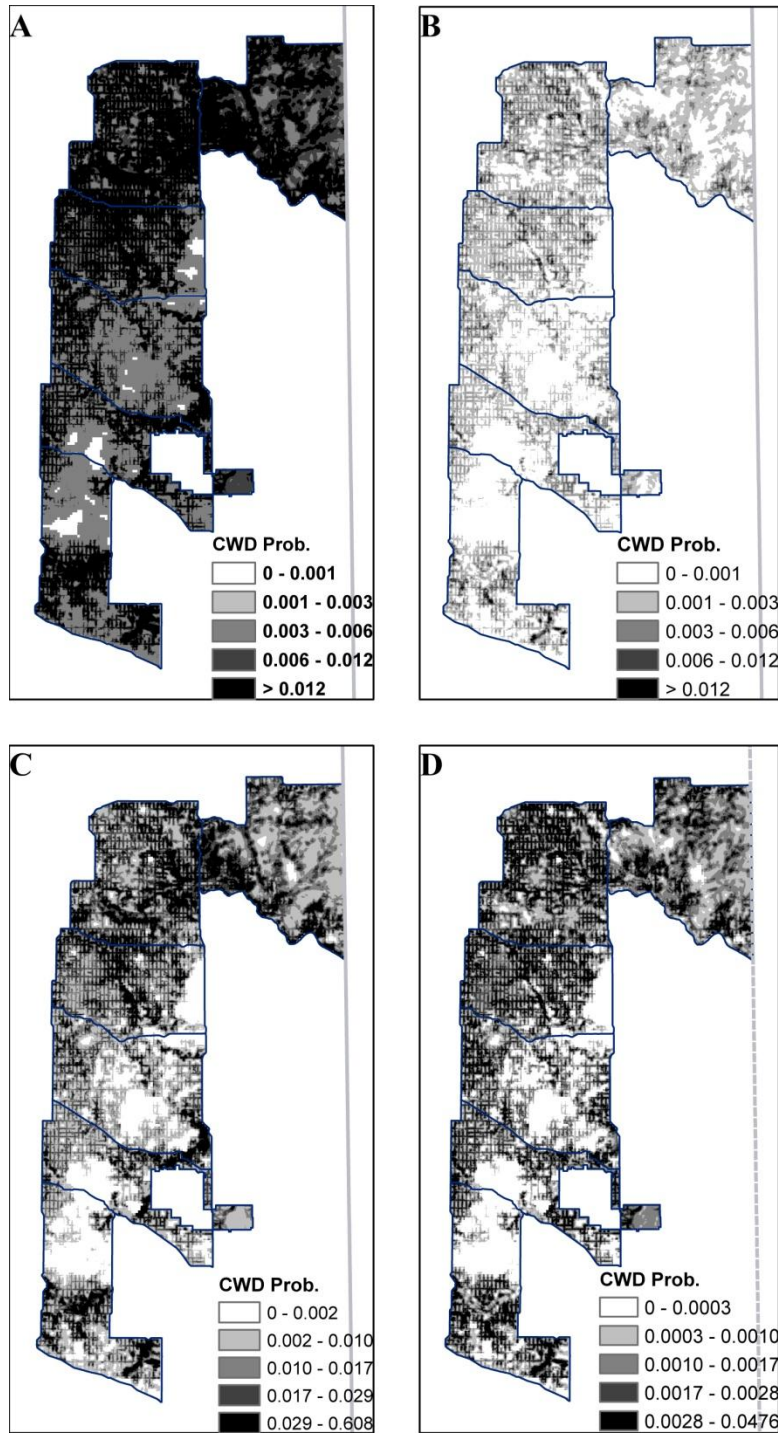


Fig. 2.7. CWD risk maps for 7 Alberta WMUs (203, 730, 232, 238, 254, 258 and 500) based on the P_{IDM} risk models with risk values weighted by species and sex proportions based on male mule deer (A, C) or female white-tailed deer (B, D) where A and B P_{IDM} values share the same values that denote pixel shading to highlight the difference in risk values between the two maps. While the C and D pixel values are adjusted to make relative value rankings the same by using equal area bins.

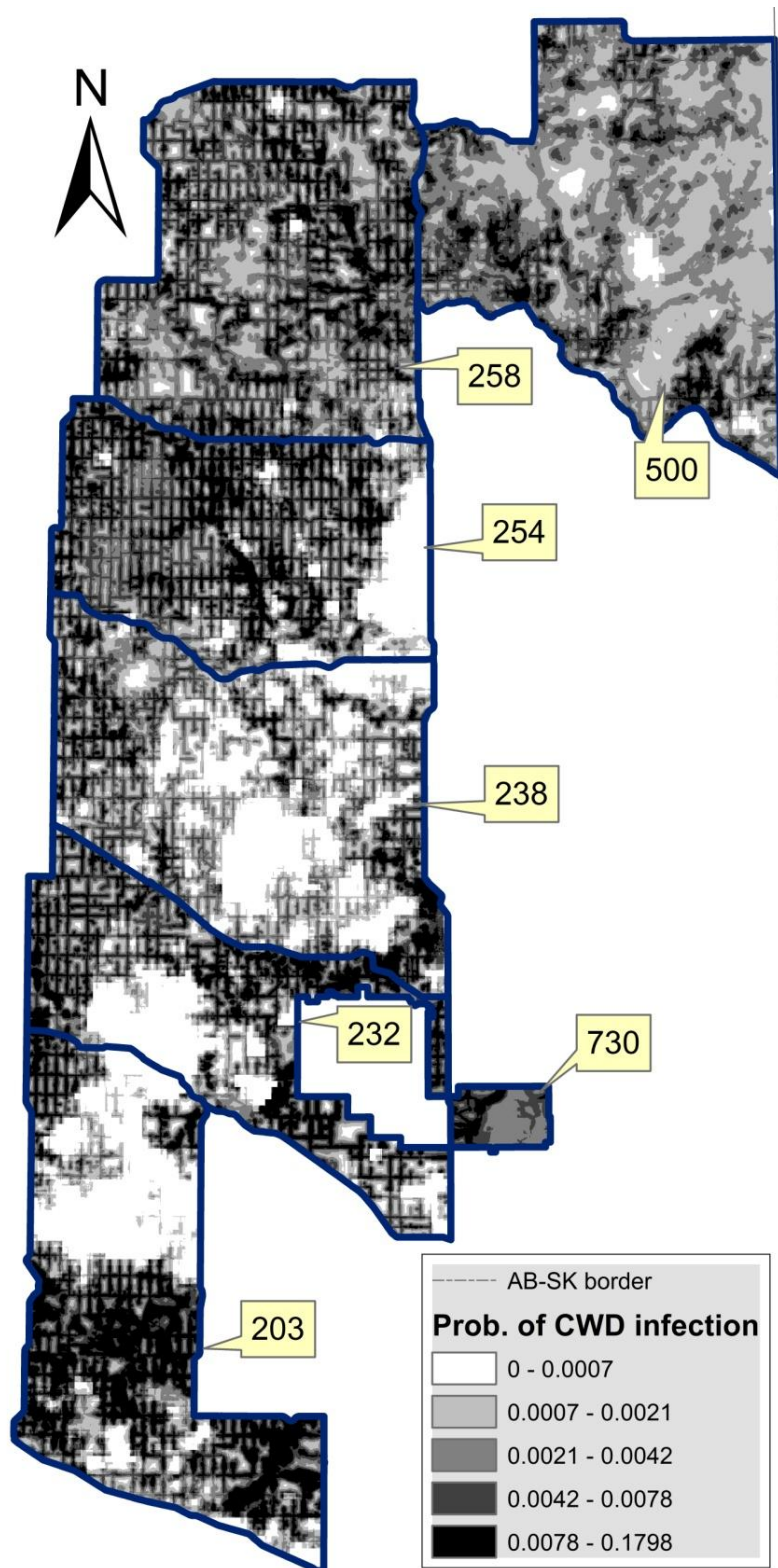


Fig. 2.8. CWD risk map for 7 WMUs (203, 730, 232, 238, 254, 258 and 500) based on the predictions of the P_{IDM} risk model with species and sex weightings proportional to estimated herd compositions specific to each WMU. The year in the P_{IDM} is set to 2011.

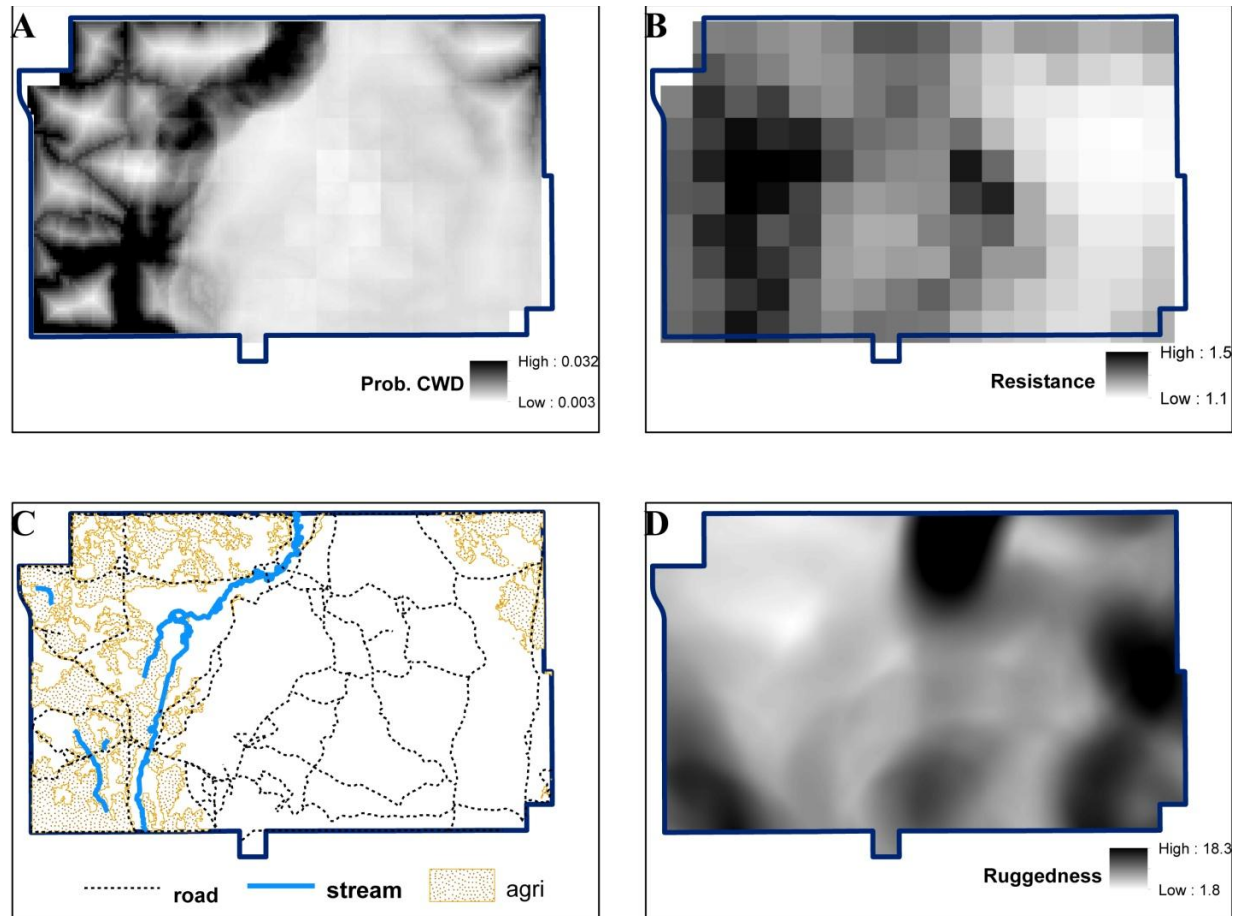


Fig. 2.9. A) CWD risk map for wildlife management unit 730 based on the P_{IDM} risk model with species and sex weightings proportional to estimated herd composition, and landscape covariate inputs for deriving P_{IDM} ; B) Average landscape resistance to previously detected CWD cases ($M_{Resistance}$), C) Streams, roads and agriculture and D) Terrain ruggedness ($Rugg_{12km}$).

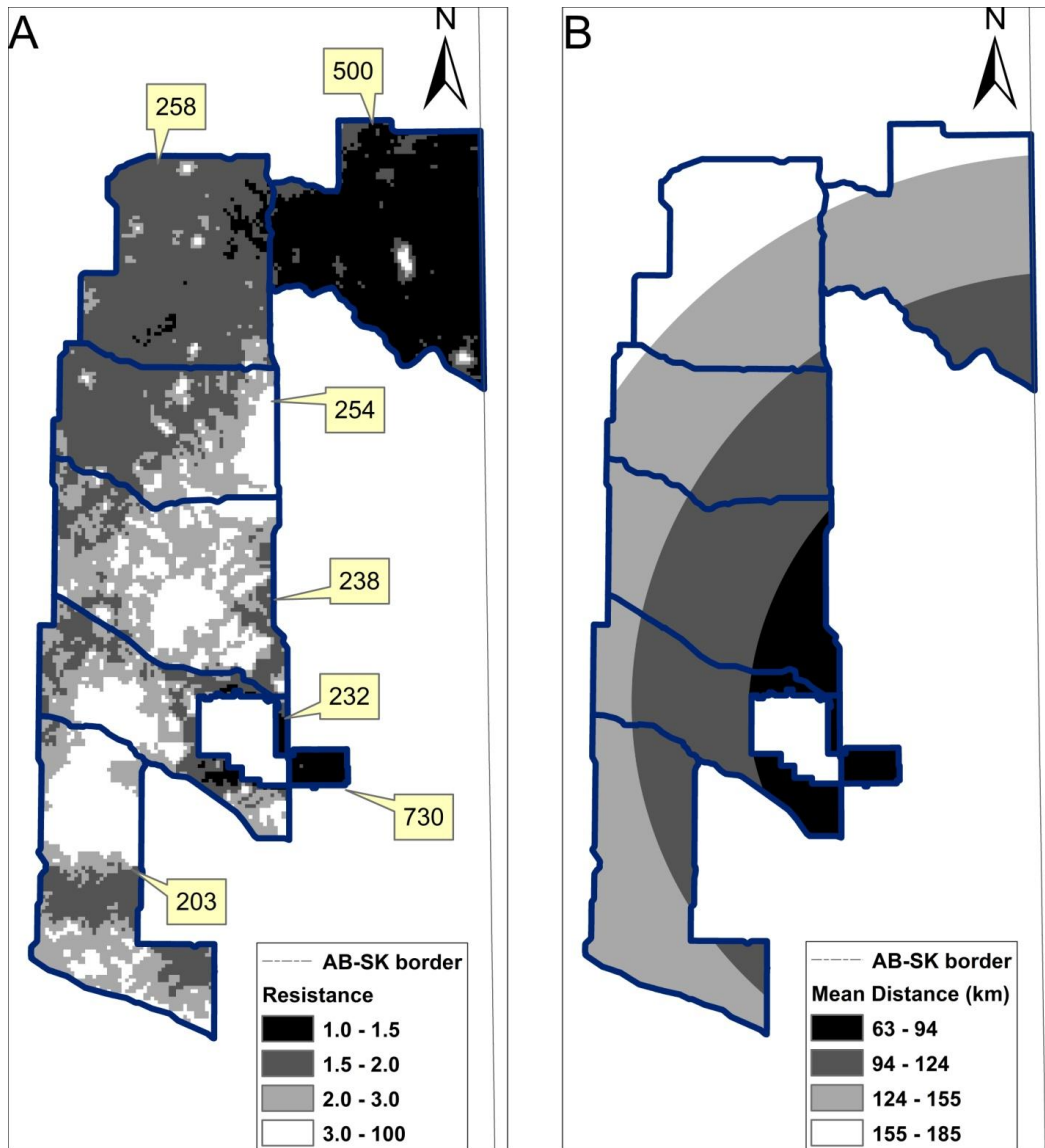


Fig. 2.10. A) Landscape resistance, which is the inverse of connectivity ($M_{Resistance}$) and B) mean distance (km) to previously detected CWD+ cases mapped for the 7 "disease-free" WMUs (203, 730, 232, 238, 254, 258 and 500). Resistance is based on a combination of a step selection function for mule deer and circuit theory.

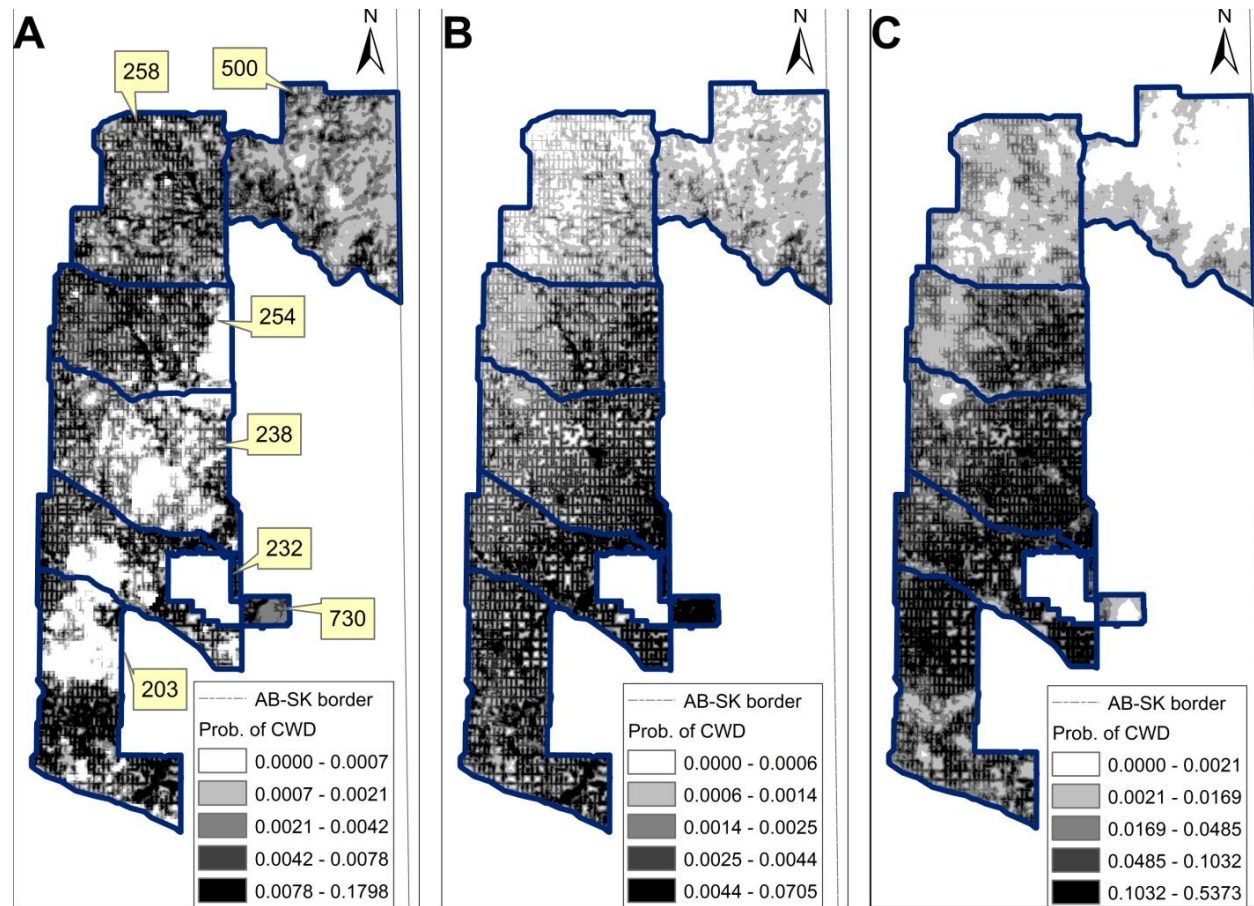


Fig. 2.11. CWD risk map for 7 WMUs (203, 730, 232, 238, 254, 258 and 500) based on: A) P_{IDM} risk model, B) P_{IDM} with proximity covariate and C) P_{IDM} with proximity and quadratic for agriculture covariate. All risk predictions are weighted by species and sex proportional to estimated herd compositions specific to each WMU with year set to 2011. For each map, P_{IDM} values are grouped into 5 quantile bins for comparing relative values across maps.

Literature Cited

- Acton, D.F., Padbury, G.A. & Stushnoff, C.T. (1998) *The Ecoregions of Saskatchewan*, Regina, Sask, University of Regina, Canadian Plains Research Center.
- Agriculture and Agri-Food Canada. (2010) Land Cover for Agricultural Regions of Canada circa 2000. <http://www4.agr.gc.ca/AAFC-AAC/display-afficher.do?id=1227733122679&lang=eng> [Accessed 12 May 2010]
- Almberg, E.S., Cross, P.C., Johnson, C.J., Heisey, D.M. & Richards, B.J. (2011) Modeling routes of chronic wasting disease transmission: Environmental prion persistence promotes deer population decline and extinction. *Plos One*, **6**, e19896.
- Anderson, D.R. (2008) *Model Based Inference in the Life Sciences: A Primer on Evidence*, New York, Springer.
- Anderson, E.D., Long, R.A., Atwood, M.P., Kie, J.G., Thomas, T.R., Zager, P. & Bowyer, R.T. (2012) Winter resource selection by female mule deer *odocoileus hemionus*: Functional response to spatio-temporal changes in habitat. *Wildlife Biology*, **18**, 153-163.
- Archie, E.A., Luikart, G. & Ezenwa, V.O. (2009) Infecting epidemiology with genetics: A new frontier in disease ecology. *Trends in Ecology & Evolution*, **24**, 21-30.
- Austerlitz, F., JungMuller, B., Godelle, B. & Gouyon, P. (1997) Evolution of coalescence times, genetic diversity and structure during colonization. *Theoretical Population Biology*, **51**, 148-164.
- Bar-David, S., Lloyd-Smith, J.O. & Getz, W.M. (2006) Dynamics and management of infectious disease in colonizing populations. *Ecology*, **87**, 1215-1224.
- Barrett, M.W., Nolan, J.W. & Roy, L.D. (1982) Evaluation of a hand-held net-gun to capture large mammals. *Wildlife Society Bulletin*, **10**, 108-114.
- Batschelet, E. (1981) *Circular Statistics in Biology*, London; Toronto, Academic Press.
- Begon, M., Bennett, M., Bowers, R.G., French, N.P., Hazel, S.M. & Turner, J. (2002) A clarification of transmission terms in host-microparasite models: Numbers, densities and areas. *Epidemiology and Infection*, **129**, 147-153.

- Biek, R. & Real, L.A. (2010) The landscape genetics of infectious disease emergence and spread. *Molecular Ecology*, **19**, 3515-3531.
- Bird, R.D. (1961) Ecology of the Aspen Parkland of Western Canada in Relation to Land Use. *Canada Department of Agriculture, Ottawa, Ontario, Canada*.
- Blanchong, J.A., Samuel, M.D., Scribner, K.T., Weckworth, B.V., Langenberg, J.A. & Filcek, K.B. (2008) Landscape genetics and the spatial distribution of chronic wasting disease. *Biology Letters*, **4**, 130-133.
- Bowyer, R.T. (1984) Sexual segregation in southern mule deer. *Journal of Mammalogy*, **65**, 410-417.
- Bowyer, R. (1986) Habitat selection by southern mule deer. *California Fish and Game*, **72**, 153-169.
- Bowyer, R., Van Ballenberghe, V., Kie, J. & Maier, J. (1999) Birth-site selection by alaskan moose: Maternal strategies for coping with a risky environment. *Journal of Mammalogy*, **80**, 1070-1083.
- Brown, J. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography - effect of immigration on extinction. *Ecology*, **58**, 445-449.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. New York, Springer.
- Canadian Cooperative Wildlife Health Centre. (2011) A Proposal for Canada's National Chronic Wasting Disease Control Strategy.
http://www.ccwhc.ca/publications/A_Proposal_for_a_National_CWD_Control_Strategy_2011_final.pdf
- Chetkiewicz, C.B. & Boyce, M.S. (2009) Use of resource selection functions to identify conservation corridors. *Journal of Applied Ecology*, **46**, 1036-1047.
- Chiu, J., Wobeser, G. & Bollinger, T. (2009) Granulomatous inflammation in retropharyngeal lymph nodes of wild cervids in saskatchewan. *Journal of Wildlife Diseases*, **45**, 625-630.
- Clements, G.M., Hygnstrom, S.E., Gilsdorf, J.M., Baasch, D.M., Clements, M.J. & Vercauteren, K.C. (2011) Movements of white-tailed deer in riparian habitat: Implications for infectious diseases. *Journal of Wildlife Management*, **75**, 1436-1442.

- Clobert, J., Le Galliard, J., Cote, J., Meylan, S. & Massot, M. (2009) Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters*, **12**, 197-209.
- Clover, M.R. (1954) A portable deer trap and catch-net. *California Fish and Game*, **40**, 367-373.
- Conner, M.M. & Miller, M.W. (2004) Movement patterns and spatial epidemiology of a prion disease in mule deer population units. *Ecological Applications*, **14**, 1870-1881.
- Conner, M.M., Gross, J.E., Cross, P.C., Ebinger, M.R., Gillies, R.R. & Miller, M.W. (2007) Scale-dependent approaches to modeling spatial epidemiology of chronic wasting disease. *Ecological Applications*, **17**, 140-153.
- Coulon, A., Morellet, N., Goulard, M., Cargnelutti, B., Angibault, J. & Hewison, A.J.M. (2008) Inferring the effects of landscape structure on roe deer (*capreolus capreolus*) movements using a step selection function. *Landscape Ecology*, **23**, 603-614.
- Cullingham, C.I., Nakada, S.M., Merrill, E.H., Bollinger, T.K., Pybus, M.J. & Coltman, D.W. (2011a) Multiscale population genetic analysis of mule deer (*odocoileus hemionus hemionus*) in western canada sheds new light on the spread of chronic wasting disease. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **89**, 134-147.
- Cullingham, C.I., Merrill, E.H., Pybus, M.J., Bollinger, T.K., Wilson, G.A. & Coltman, D.W. (2011b) Broad and fine-scale genetic analysis of white-tailed deer populations: Estimating the relative risk of chronic wasting disease spread. *Evolutionary Applications*, **4**, 116-131.
- Cushman, S.A. & Lewis, J.S. (2010) Movement behavior explains genetic differentiation in american black bears. *Landscape Ecology*, **25**, 1613-1625.
- Dale, M.R.T. & Fortin, M. (2010) From graphs to spatial graphs. *Annual Review of Ecology, Evolution, and Systematics*, Vol 41, **41**, 21-38.
- Dierauf, L. & Fischer, J. (2005) CWD found in both free-ranging and captive deer in New York. USGS.
http://www.nwhc.usgs.gov/publications/wildlife_health_bulletins/WHB_05_01.jsp [Accessed 1 July 2011]
- Eberhardt, L., Hanson, E. & Cadwell, L. (1984) Movement and activity patterns of mule deer in the sagebrush-steppe region. *Journal of Mammalogy*, **65**, 404-409.

- ESRI. (2009) Cell size and resampling in analysis. *ArcGIS Desktop 9.3 Help*, http://webhelp.esri.com/arcgisdesktop/9.3/index.cfm?TopicName=Cell_size_and_resampling_in_analysis [Accessed 3 March 2012].
- Farnsworth, M.L., Wolfe, L.L., Hobbs, N.T., Burnham, K.P., Williams, E.S., Theobald, D.M., Conner, M.M. & Miller, M.W. (2005) Human land use influences chronic wasting disease prevalence in mule deer. *Ecological Applications*, **15**, 119-126.
- Festa-Bianchet, M. (1988) Seasonal range selection in bighorn sheep - conflicts between forage quality, forage quantity, and predator avoidance. *Oecologia*, **75**, 580-586.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.
- Fischhoff, I.R., Sundaresan, S.R., Cordingley, J. & Rubenstein, D.I. (2007) Habitat use and movements of plains zebra (*equus burchelli*) in response to predation in danger from lions. *Behavioral Ecology*, **18**, 725-729.
- Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005) Wolves influence elk movements: Behavior shapes a trophic cascade in yellowstone national park. *Ecology*, **86**, 1320-1330.
- Foster, J., Roseberry, J. & Woolf, A. (1997) Factors influencing efficiency of white-tailed deer harvest in illinois. *Journal of Wildlife Management*, **61**, 1091-1097.
- Garlick, M.J., Powell, J.A., Hooten, M.B. & McFarlane, L.R. (2011) Homogenization of large-scale movement models in ecology. *Bulletin of Mathematical Biology*, **73**, 2088-2108.
- Gavier-Widen, D., Stack, M.J., Baron, T., Balachandran, A. & Simmons, M. (2005) Diagnosis of transmissible spongiform encephalopathies in animals: A review. *Journal of Veterinary Diagnostic Investigation*, **17**, 509-527.
- Gilbert, M., Mitchell, A., Bourn, D., Mawdsley, J., Cliton-Hadley, R. & Wint, W. (2005) Cattle movements and bovine tuberculosis in great britain. *Nature*, **435**, 491-496.
- Gillies, C.S., Beyer, H.L. & St Clair, C.C. (2011) Fine-scale movement decisions of tropical forest birds in a fragmented landscape. *Ecological Applications*, **21**, 944-954.

- Greer, A.L. & Collins, J.P. (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.
- Grovenburg, T.W., Swanson, C.C., Jacques, C.N., Deperno, C.S., Klaver, R.W. & Jenks, J.A. (2011) Female white-tailed deer survival across ecoregions in minnesota and south dakota RID B-7321-2009. *American Midland Naturalist*, **165**, 426-435.
- Habib, T.J., Merrill, E.H., Pybus, M.J. & Coltman, D.W. (2011) Modelling Landscape Effects on Density-contact Rate Relationships of Deer in eastern Alberta: Implications for Chronic Wasting Disease. *Ecological Modelling*, **222**, 2722-2732.
- Habib, T.J., Moore, D.A., & Merrill, E.H. (in press) Detection and stratification approaches for aerial surveys of deer in prairie-parklands. *Wildlife Research*, in press.
- Heisey, D.M., Osnas, E.E., Cross, P.C., Joly, D.O., Langenberg, J.A. & Miller, M.W. (2010) Linking process to pattern: Estimating spatiotemporal dynamics of a wildlife epidemic from cross-sectional data. *Ecological Monographs*, **80**, 221-240.
- Hess, G. (1996) Disease in metapopulation models: Implications for conservation. *Ecology*, **77**, 1617-1632.
- Hess, G.R., Randolph, E., Arnberg, P., Chemini, C., Furlanello, C., Harwood, J., Roberts, G. & Swinton, J. (2002) Spatial aspects of disease dynamics. *The Ecology of Wildlife Diseases* Anonymous pp. 102-118. New York, Oxford University Press.
- Hess, G. (1994) Conservation corridors and contagious-disease - a cautionary note. *Conservation Biology*, **8**, 256-262.
- Hutchison, D. & Templeton, A. (1999) Correlation of pairwise genetic and geographic distance measures: Inferring the relative influences of gene flow and drift on the distribution of genetic variability. *Evolution*, **53**, 1898-1914.
- Imai, K., King, G. & Lau, O. (2011) Zelig: Everyone's statistical software. <http://GKing.Harvard.edu/zelig>
- Imai, K., King, G. & Lau, O. (2008) Toward a common framework for statistical analysis and development. *Journal of Computational and Graphical Statistics*, **4**, 892-913.

- Inglis, J., Hood, R., Brown, B. & Deyoung, C. (1979) Home range of white-tailed deer in texas coastal prairie brushland. *Journal of Mammalogy*, **60**, 377-389.
- Jackson, V., Huntley, S., Tomlinson, A., Smith, G.C., Taylor, M. & Delahay, R. (2008) Risk assessment and contingency planning for exotic disease introductions . *Management of Disease in Wild Mammals* Anonymous pp. 169-185. Tokyo; London, Springer.
- Joly, D.O., Samuel, M.D., Langenberg, J.A., Blanchong, J.A., Batha, C.A., Rolley, R.E., Keane, D.P. & Ribic, C.A. (2006) Spatial epidemiology of chronic wasting disease in wisconsin white-tailed deer. *Journal of Wildlife Diseases*, **42**, 578-588.
- King, G. & Zeng, L. (2001) Logistic regression in rare events data. *Political Analysis*, **9**, 137-163.
- Kjaer, L.J., Schaubert, E.M. & Nielsen, C.K. (2008) Spatial and temporal analysis of contact rates in female white-tailed deer. *Journal of Wildlife Management*, **72**, 1819-1825.
- Koen, E.L., Garroway, C.J., Wilson, P.J. & Bowman, J. (2010) The effect of map boundary on estimates of landscape resistance to animal movement. *Plos One*, **5**, e11785.
- La Morgia, V., Malenotti, E., Badino, G. & Bona, F. (2011) Where do we go from here? dispersal simulations shed light on the role of landscape structure in determining animal redistribution after reintroduction. *Landscape Ecology*, **26**, 969-981.
- Lang, K.R. & Blanchong, J.A. (2012) Population genetic structure of white-tailed deer: Understanding risk of chronic wasting disease spread. *Journal of Wildlife Management*, **76**, 832-840.
- Langenberg, J.A., Miller, M.W. & Creekmore, L. (2008) *Alberta Chronic Wasting Disease Management Program Review Panel Report*. <http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/documents/AlbertaCWDMManagement-ProgramReviewPanelReport-Feb2008.pdf>
- Lingle, S. (2003) Group composition and cohesion in sympatric white-tailed deer and mule deer. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **81**, 1119-1130.
- Lingle, S. (2002) Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, **83**, 2037-2048.

- Lingle, S. (1993) Escape gaits of white-tailed deer, mule deer, and their hybrids - body configuration, biomechanics, and function. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **71**, 708-724.
- Lingle, S. (1992) Escape gaits of white-tailed deer, mule deer and their hybrids - gaits observed and patterns of limb coordination. *Behaviour*, **122**, 153-181.
- Lingle, S. & Pellis, S.M. (2002) Fight or flight? antipredator behavior and the escalation of coyote encounters with deer. *Oecologia*, **131**, 154-164.
- Long, E.S., Diefenbach, D.R., Rosenberry, C.S., Wallingford, B.D. & Grund, M.R.D. (2005) Forest cover influences dispersal distance of white-tailed deer. *Journal of Mammalogy*, **86**, 623-629.
- Long, E.S., Diefenbach, D.R., Wallingford, B.D. & Rosenberry, C.S. (2010) Influence of roads, rivers, and mountains on natal dispersal of white-tailed deer. *Journal of Wildlife Management*, **74**, 1242-1249.
- McKenzie, H.W., Merrill, E.H., Spiteri, R.J. & Lewis, M.A. (2012) How linear features alter predator movement and the functional response. *Interface Focus*, **2**, 205-216.
- McRae, B.H. (2006) Isolation by resistance. *Evolution*, **60**, 1551-1561.
- McRae, B.H. & Beier, P. (2007) Circuit theory predicts gene flow in plant and animal populations. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 19885-19890.
- McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, **89**, 2712-2724.
- Meentemeyer, R.K., Anacker, B.L., Mark, W. & Rizzo, D.M. (2008) Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. *Ecological Applications*, **18**, 377-390.
- Menard, S. (2004) Six approaches to calculating standardized logistic regression coefficients. *American Statistician*, **58**, 218-223.
- Meyers, L., Pourbohloul, B., Newman, M., Skowronski, D. & Brunham, R. (2005) Network theory and SARS: Predicting outbreak diversity. *Journal of Theoretical Biology*, **232**, 71-81.
- Miller, M.W. & Williams, E.S. (2003) Horizontal prion transmission in mule deer. *Nature*, **425**, 35-36.

- Miller, M.W., Williams, E.S., Hobbs, N.T. & Wolfe, L.L. (2004) Environmental sources of prion transmission in mule deer. *Emerging Infectious Diseases*, **10**, 1003-1006.
- Miller, M.W., Williams, E.S., McCarty, C.W., Spraker, T.R., Kreeger, T.J., Larsen, C.T. & Thorne, E.T. (2000) Epizootiology of chronic wasting disease in free-ranging cervids in colorado and wyoming. *Journal of Wildlife Diseases*, **36**, 676-690.
- Miller, M.W., Hobbs, N.T. & Tavener, S.J. (2006) Dynamics of prion disease transmission in mule deer. *Ecological Applications*, **16**, 2208-2214.
- Nelson, M.E. (1998) Development of migratory behavior in northern white-tailed deer. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **76**, 426-432.
- Nelson, M.E., Mech, L.D. & Frame, P.F. (2004) Tracking of white-tailed deer migration by global positioning system. *Journal of Mammalogy*, **85**, 505-510.
- Nelson, M. (1993) Natal dispersal and gene flow in white-tailed deer in northeastern minnesota. *Journal of Mammalogy*, **74**, 316-322.
- New York State DEC. (2012) Status of chronic wasting disease in NY. *New York State Department of Environmental Conservation Website*, <http://www.dec.ny.gov/animals/33220.html> [Accessed 1 July 2012]
- Nixon, C.M., Mankin, P.C., Etter, D.R., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Esker, T.L. & Sullivan, J.B. (2008) Migration behavior among female white-tailed deer in central and northern illinois. *American Midland Naturalist*, **160**, 178-190.
- Nixon, C.M., Mankin, P.C., Etter, D.R., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Esker, T.L. & Sullivan, J.B. (2007) White-tailed deer dispersal behavior in an agricultural environment. *American Midland Naturalist*, **157**, 212-220.
- Nixon, C., Hansen, L., Brewer, P. & Chelsvig, J. (1991) Ecology of white-tailed deer in an intensively farmed region of illinois. *Wildlife Monographs*, **118**, 3-77.
- Osnas, E.E., Heisey, D.M., Rolley, R.E. & Samuel, M.D. (2009) Spatial and temporal patterns of chronic wasting disease: Fine-scale mapping of a wildlife epidemic in wisconsin. *Ecological Applications*, **19**, 1311-1322.

- Oyer, A.M., Mathews, N.E. & Skuldt, L.H. (2007) Long-distance movement of a white-tailed deer away from a chronic wasting disease area. *Journal of Wildlife Management*, **71**, 1635-1638.
- Palomares, F., Delibes, M., Ferreras, P., Fedriani, J.M., Calzada, J. & Revilla, E. (2000) Iberian lynx in a fragmented landscape: Predispersal, dispersal, and postdispersal habitats. *Conservation Biology*, **14**, 809-818.
- Pauley, G.R., Peek, J.M. & Zager, P. (1993) Predicting white-tailed deer habitat use in northern idaho. *Journal of Wildlife Management*, **57**, 904-913.
- Pierce, B., Bowyer, R. & Bleich, V. (2004) Habitat selection by mule deer: Forage benefits or risk of predation? *Journal of Wildlife Management*, **68**, 533-541.
- Potapov, A., Merrill, E.H., Pybus, M., Coltman, D.W. & Lewis, M. (2011) Chronic wasting disease: On possible transmission mechanisms in deer. *Proceedings of the Royal Society*, **279**, 3139-3145.
- Proctor, M.F., Paetkau, D., Mclellan, B.N., Stenhouse, G.B., Kendall, K.C., Mace, R.D., Kasworm, W.F., Servheen, C., Lausen, C.L., Gibeau, M.L., Wakkinen, W.L., Haroldson, M.A., Mowat, G., Apps, C.D., Ciarniello, L.M., Barclay, R.M.R., Boyce, M.S., Schwartz, C.C. & Strobeck, C. (2012) Population fragmentation and inter-ecosystem movements of grizzly bears in western canada and the northern united states. *Wildlife Monographs*, **180**, 1-46.
- R Development Core Team. (2011) *R: A Language and Environment for Statistical Computing*, Vienna, Austria, R Foundation for Statistical Computing.
- Rees, E.E., Merrill, E.H., Bollinger, T.K., Ten Hwang, Y., Pybus, M.J. & Coltman, D.W. (2012) Targeting the detection of chronic wasting disease using the hunter harvest during early phases of an outbreak in saskatchewan, canada. *Preventive Veterinary Medicine*, **104**, 149-159.
- Rees, E.E., Pond, B.A., Cullingham, C.I., Tinline, R., Ball, D., Kyle, C.J. & White, B.N. (2008) Assessing a landscape barrier using genetic simulation modelling: Implications for raccoon rabies management. *Preventive Veterinary Medicine*, **86**, 107-123.
- Remais, J., Akullian, A., Ding, L. & Seto, E. (2010) Analytical methods for quantifying environmental connectivity for the control and surveillance of infectious disease spread. *Journal of the Royal Society Interface*, **7**, 1181-1193.

- Robinett, W.L. (1966) Mule deer home range and dispersal in Utah. *Journal of Wildlife Management*, **30**, 335-345.
- Roever, C.L., Boyce, M.S. & Stenhouse, G.B. (2010) Grizzly bear movements relative to roads: Application of step selection functions. *Ecography*, **33**, 1113-1122.
- Rogers, W.H. (1993) Regression standard errors in clustered samples. *Stata Technical Bulletin*, **13**, 19-23.
- Root, J.J., Puskas, R.B., Fischer, J.W., Swope, C.B., Neubaum, M.A., Reeder, S.A. & Piaggio, A.J. (2009) Landscape genetics of raccoons (*Procyon lotor*) associated with ridges and valleys of Pennsylvania: Implications for oral rabies vaccination programs. *Vector-Borne and Zoonotic Diseases*, **9**, 583-588.
- Russell, C., Smith, D., Waller, L., Childs, J. & Real, L. (2004) A priori prediction of disease invasion dynamics in a novel environment RID B-2226-2008. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **271**, 21-25.
- Samuel, M.D., Joly, D.O., Wild, M.A., Wright, S.D., Otis, D.L., Werge, R.W. & Miller, M.W. (2003) *Surveillance Strategies for Detecting Chronic Wasting Disease in Free-Ranging Deer and Elk*, edn. Madison, Wisconsin, US Geological Survey—National Wildlife Health Center.
http://www.nwhc.usgs.gov/publications/fact_sheets/pdfs/cwd/CWD_Surveillance_Strategies.pdf
- Saunders, S.E., Bartz, J.C. & Bartelt-Hunt, S.L. (2012a) Soil-mediated prion transmission: Is local soil-type a key determinant of prion disease incidence? *Chemosphere*, **87**, 661-667.
- Saunders, S.E., Bartelt-Hunt, S.L. & Bartz, J.C. (2012b) Occurrence, transmission, and zoonotic potential of chronic wasting disease. *Emerging Infectious Diseases*, **18**, 369-376.
- Saunders, S.E., Shikiya, R.A., Langenfeld, K., Bartelt-Hunt, S.L. & Bartz, J.C. (2011) Replication efficiency of soil-bound prions varies with soil type. *Journal of Virology*, **85**, 5476-5482.
- Sawyer, H., Nielson, R., Lindzey, F. & McDonald, L. (2006) Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management*, **70**, 396-403.

- Sawyer, H., Kauffman, M.J., Nielson, R.M. & Horne, J.S. (2009) Identifying and prioritizing ungulate migration routes for landscape-level conservation. *Ecological Applications*, **19**, 2016-2025.
- Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, **73**, 1052-1061.
- Schreiber, S.J. & Lloyd-Smith, J.O. (2009) Invasion dynamics in spatially heterogeneous environments. *American Naturalist*, **174**, 490-505.
- Selonen, V. & Hanski, I.K. (2006) Habitat exploration and use in dispersing juvenile flying squirrels. *Journal of Animal Ecology*, **75**, 1440-1449.
- Shelton, P. & McDonald, P. (2011) Illinois chronic wasting disease: 2010-2011 Surveillance/Management summary. *Illinois Department of Natural Resources*, <http://dnr.state.il.us/cwd/Documents/CWDAnnualReport20102011.pdf>.
- Silbernagel, E. (2010) *Factors affecting the movement patterns of mule deer (odocoileus hemionus) in southern saskatchewan: Implications for chronic wasting disease spread*. M.Sc., University of Saskatchewan, Saskatoon, Saskatchewan.
- Silbernagel, E., Skelton, N., Waldner, C. & Bollinger, T. (2011) Interaction among deer in a chronic wasting disease endemic zone. *Journal of Wildlife Management*, **75**, 1453-1461.
- Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. (2005) ROCr: Visualizing classifier performance in R. *Bioinformatics*, **21**, 3940-3941.
- Skuldt, L.H., Mathews, N.E. & Oyer, A.M. (2008) White-tailed deer movements in a chronic wasting disease area in south-central wisconsin. *Journal of Wildlife Management*, **72**, 1156-1160.
- Smith, C.B., Booth, C.J. & Pedersen, J.A. (2011) Fate of prions in soil: A review. *Journal of Environmental Quality*, **40**, 449-461.
- Smith, D.L., Lucey, B., Waller, L.A., Childs, J.E. & Real, L.A. (2002) Predicting the spatial dynamics of rabies epidemics on heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 3668-3672.
- Spear, S.F., Balkenhol, N., Fortin, M., McRae, B.H. & Scribner, K. (2010) Use of resistance surfaces for landscape genetic studies: Considerations for parameterization and analysis. *Molecular Ecology*, **19**, 3576-3591.

- StataCorp. 2007. *Stata Statistical Software: Release 10*. College Station, TX: StataCorp LP.
- Urban, D.L., Minor, E.S., Treml, E.A. & Schick, R.S. (2009) Graph models of habitat mosaics. *Ecology Letters*, **12**, 260-273.
- Vaclavik, T., Kanaskie, A., Hansen, E.M., Ohmann, J.L. & Meentemeyer, R.K. (2010) Predicting potential and actual distribution of sudden oak death in oregon: Prioritizing landscape contexts for early detection and eradication of disease outbreaks. *Forest Ecology and Management*, **260**, 1026-1035.
- Vander Wal, E., Paquet, P.C. & Andres, J.A. (2012) Influence of landscape and social interactions on transmission of disease in a social cervid. *Molecular Ecology*, **21**, 1271-1282.
- Walsh, D.P. & Miller, M.W. (2010) A weighted surveillance approach for detecting chronic wasting disease foci. *Journal of Wildlife Diseases*, **46**, 118-135.
- Walter, W.D., Walsh, D.P., Farnsworth, M.L., Winkelman, D.L. & Miller, M.W. (2011a) Soil clay content underlies prion infection odds. *Nature Communications*, **2**, 200.
- Walter, W.D., Baasch, D.M., Hygnstrom, S.E., Trindle, B.D., Tyre, A.J., Millspaugh, J.J., Frost, C.J., Boner, J.R. & VerCauteren, K.C. (2011b) Space use of sympatric deer in a riparian ecosystem in an area where chronic wasting disease is endemic. *Wildlife Biology*, **17**, 191-209.
- Wasserberg, G., Osnas, E.E., Rolley, R.E. & Samuel, M.D. (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.
- Wilcox, B. & Murphy, D. (1985) Conservation strategy - the effects of fragmentation on extinction. *American Naturalist*, **125**, 879-887.
- Williams, E.S. & Miller, M.W. (2003) Prions in the wild: CWD in deer and elk. *Microbiology Today*, **30**, 172-173.
- Williams, E.S., Miller, M.W., Kreeger, T.J., Kahn, R.H. & Thorne, E.T. (2002) Chronic wasting disease of deer and elk: A review with recommendations for management. *Journal of Wildlife Management*, **66**, 551-563.
- Williams, R.L. (2000) A note on robust variance estimation for cluster-correlated data. *Biometrics*, **56**, 645-646.

Wishart, W. (1984) Western Canada. *White-Tailed Deer : Ecology and Management* (ed L.K. Halls), pp. 475-486. Harrisburg, PA, Stackpole Books.

Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn. Upper Saddle River, N.J, Prentice Hall.

CHAPTER 3

A TALE OF TWO SPECIES: COMPARING SOURCE-SINK HABITAT BETWEEN MULE AND WHITE-TAILED DEER

Introduction

Habitat selection and species occurrence models are used extensively for conservation and management purposes because they are assumed to identify quality habitat (Guisan & Thuiller 2005; Jensen *et al.* 2008; Qi *et al.* 2012). However, these metrics do not always reflect the fitness of the animals using them (Morrison 2001; Gilroy *et al.* 2011). As a result, an alternative approach to assessing habitat quality has now been developed based on both, habitat selection and the fitness consequences of using that habitat (Naves *et al.* 2003; Nielsen *et al.* 2006). This approach identifies areas likely to be selected that also result in high reproduction and survival, designated as source habitat (Pulliam 1988; Dias 1996), and conversely areas that are selected but result in low reproduction and survival, designated as sink habitat (Delibes *et al.* 2001; Fletcher *et al.* 2012).

To date, applications of this approach have focused on identifying source-sink habitats using only survival or reproduction, yet fitness is dependent on both (Griffin & Mills 2009). Extending these source-sink analyses based on the consequences for both survival and reproduction, may allow for a more complete understanding of habitat quality. Further, applications have been restricted to endangered species like greater sage-grouse (*Centrocercus urophasianus*, Aldridge & Boyce 2007) and brown bears (*Ursus arctos*, Falcucci *et al.* 2009)

because of the emphasis on critical habitats for preventing loss of small populations. However, the approach may prove useful for a broader range of species including large ungulates, whose spatial variation in fitness may necessitate local management actions, such as providing greater hunting opportunities, reducing crop damage, or controlling the spread of disease (Allombert *et al.* 2005; Langenberg *et al.* 2008; Knight *et al.* 2009; Hansen 2011)

In this Chapter, I compare the spatial distribution of source-sink habitats for mule deer (*Odocoileus hemionus*) and white-tailed deer (*O. virginianus*) as a first step in linking habitat characteristics to populations for predicting the spatial spread of chronic wasting disease (CWD). Potapov *et al.* (2012) found that survival and recruitment influence prevalence rates and likelihood of disease eradication using non-spatial CWD models. Specifically, increased mortality rates reduce CWD prevalence by removing infected individuals prior to them transmitting the disease to healthy deer. While a high recruitment rate can reduce prevalence by diluting the proportion of infected individuals within the population. Further study of the spatial variation in survival and recruitment within deer habitat, via the identification of sources and sinks, would help to inform future spatially explicit CWD spread models of the consequences of habitat on disease transmission and prevalence.

To identify source and sink areas in east-central Alberta for these two deer species, I generally followed the approach of Nielsen *et al.* (2006) by combining the probability that an area is selected with probabilities of fitness. However, I derived three source-sink evaluations that were related to seasonal habitat

selection and fitness metrics for pregnancy, hunting mortality and non-hunting mortality. The focus of identifying source-sink habitat was on adult, female deer because they have a disproportionately high influence on the population growth rate (Gaillard *et al.* 2000; Gaillard *et al.* 2010). For pregnancy, I focused on summer habitats because ungulates can compensate for loss of body reserves during winter (Cook *et al.* 2004; Hurley *et al.* 2011), and those that reach high body fat by fall have higher pregnancy rates or number of fetuses (Mitchell *et al.* 1976, Johnstone-Yellin *et al.* 2009). Reproductive source-sink habitats were derived from models of summer habitat selection by female radio-collared deer, pregnancy rates of deer harvested during a late winter CWD surveillance program in 2005-2007 and summer use areas assumed from kill site locations.

For mortality risk, I separated risks into hunting and non-hunting because being killed by hunters has been reported to relate to hunter access (Gratson & Whitman 2000; Stedman *et al.* 2004; Farmer *et al.* 2006; Frair *et al.* 2007), less escape cover (Grovenburg *et al.* 2011) and the existence of hunting refuges (Harden *et al.* 2005; Storm *et al.* 2007). In contrast, non-hunting mortality is related to starvation, accidents, disease and predation. Deer can select for habitats that reduce either energy demands by providing thermal cover and lower snow depths that increases forage availability or reduces predation risk (DePerno *et al.* 2003; Bowyer & Kie 2009; Lishawa *et al.* 2007; DelGiudice *et al.* 2002; Delgiudice *et al.* 2006). Risk of mortality was derived from selection patterns of female collared deer in the fall (hunting mortality) and year-round (non-hunting mortality), and the probabilities of collared deer of either sex being harvested in

the fall or killed year-round. The inclusion of males into mortality risk was necessary to increase the sample of mortalities, but I assessed sex-specific habitat risk using interactions between sex and habitat covariates. Seasonal habitat selection was modeled in all cases with a resource selection probability function (RSPF, Lele 2009).

Further, Ideal Free Distribution theory predicts that animal densities should be greater in high quality habitats except under some circumstances (see Van Horne 1983). As animal densities build up in the high quality habitats, some animals are expected to move to poorer quality habitats with lower density to equalize their fitness (Fretwell & Lucas 1970). Indeed, in 93 of the 109 bird populations reviewed by Bock and Jones (2004) a positive relationship was found between density and reproductive fitness, suggesting that density is a good measure of habitat quality. As a result, higher densities of deer should be found in areas identified as source habitats than in areas indicated by mean RSPF values alone if adding a fitness component to evaluation of habitat quality is important. Therefore, I used a model selection approach to (1) evaluate whether densities of deer in winter were more related to a habitat metric based on habitat selection and fitness than on habitat selection alone, and (2) to determine the best set of components for assessing habitat quality for mule deer and white-tailed deer, assuming high deer densities indicated high habitat quality. My assessment was conducted with deer densities in winter because estimates were available only for this season. Because measurement scale can influence estimates of density (McArdle *et al.* 1990; Smallwood & Schonewald 1998), I conducted the analysis

at three scales that were all larger than the home range of deer in this region (Silbernagel *et al.* 2010). Finally, animals are expected to select for habitat that increases their fitness (Morris 2003; Morris 2011) but if they cannot perceive the poor conditions of the habitat they may actually select for habitat that reduces their fitness (Kolbe & Janzen 2002; Arlt & Part 2007; Hollander *et al.* 2011). Therefore, I also tested whether deer selected for habitat which improved their fitness.

Materials and Methods

STUDY AREA

The study site is a 13,268 km² area near Chauvin, Alberta (52°41'35.23"N, 110°08'22.23" W) along the Alberta-Saskatchewan provincial boundary. The area is aspen parkland (Bird 1961) and dominated by agricultural development (70% of land cover, Agriculture and Agri-Food Canada 2012). Undeveloped areas consist of small stands of mixed trembling aspen *Populus tremuloides* Michx. and balsam poplar *Populus balsamifera* L. forest (2%). There are also shrublands (11%) of primarily *Elaeagnus commutata* L., *Amelanchier alnifolia* Nutt., *Prunus* spp. and *Symphoricarpos* spp. and native grasslands (14%) of mainly plains rough fescue *Festuca halli* (Vasey) Piper (Acton *et al.* 1998) within undeveloped areas. The Battle River is the principal drainage along with its major tributary the Ribstone Creek. The largest lake is 9301 hectares although numerous smaller lakes, ponds and wetlands are found throughout the area (3% of land cover).

Both deer species are hunted during an archery only (3 September – 14 October), primitive weapons (15 October – 31 October) or general (1 November – 20 December) hunting season. Prior to 2008 there was no primitive weapons season, instead the archery only season extended to 31 October. Allowable harvest is regulated with an open license for white-tailed deer, but the availability of mule deer licenses is restricted by a limited draw (Data on file). However, in 2008 an open license for antlerless mule deer was instituted with the goal of increasing harvest in response to chronic wasting disease. Besides human hunters, the primary predator is coyotes (*Canis latrans* Say). Average daily temperatures from 1971 to 2000 ranged from 16.6° C in July to -14.5° C in January, with yearly cumulative precipitation averaging 408 mm (Environment Canada 2011). Winter snow pack lasted from 17 November to 10 April with an average depth of 23.1±10.1 cm (SD) in winter 2007–2008, and from 3 December to 8 April with an average depth of 19.0±11.86 cm in 2008–2009.

Deer Capture and Monitoring. A total of 128 mule deer (43 males, 85 females) and 142 white-tailed deer (41 males, 101 females) were captured using helicopter net-gunning (Barrett *et al.* 1982) or Clover traps (Clover 1954), and collared with VHF (103 white-tailed deer, 80 mule deer, LOTEK LMRT-3, Lotek Wireless, Newmarket, Ontario, Canada) or GPS-collars (39 white-tailed deer, 48 mule deer, Lotek 3300S/4400S or HABIT GPS, H.A.B.I.T Research Ltd., Victoria, BC, Canada). Male collars included a section of elastic surgical tubing to allow for neck-swelling during the mating season. Deer were monitored from 8 February 2006 to 27 February 2010, with VHF-collared deer relocated on average every

12.9 days (SD = 8.4; median = 12.0) using ground-based and aerial telemetry. GPS collars were programmed to relocate deer every 1 to 6 hr (mean = 2.1hr, SD = 1.6) and to detach after 11 months. All capture and handling protocols were approved by an animal care committee and complied with provincial permits (Univ. Alberta #4941001; Alberta Sustainable Resource Development RP: #39576, CL: 39504; Alberta Tourism, Parks, and Recreation #RC09EC003, RC09EC005; Saskatchewan Ministry of Environment #09FW028). Triangulation accuracy of locations for VHF-collared deer were not evaluated, but assumed to be within the range reported in other large mammal studies (mean = 267 m, range = 180 – 476 m, n = 6, Horner & Powell 1990; Kauhala & Tiilikainen 2002; Jones & Pelton 2003; Hebblewhite 2006; Storlie 2006; Walter *et al.* 2006). GPS collars had an average positional error of 7.5 ± 8.4 m (SD) with 1142 of 1148 fix attempts successful, based on collars hung in a stationary position at a height of 1 m for 1 to 7 days in three different vegetation types (Appendix 7).

HABITAT SELECTION

Deer Location Data. Seasonal habitat selection was modeled with a resource selection probability function (Lele & Keim 2006; Lele 2009) for adult female deer during four periods: all year, summer (1 May – 29 Nov), winter (30 Nov – 30 April) and the hunting season (3 Sept – 20 Dec). RSPFs were constructed independently for each species with GPS locations from 22 female mule deer and 24 female white-tailed deer. The same deer were monitored in all seasons, to ensure consistency for detecting seasonal changes in habitat selection.

Resource Selection Probability Function. Seasonal probability of selection was quantified using a weighted distribution approach developed by Johnson *et al.* (2006) and using software provided by Lele (2009). Because the software does not accommodate mixed models and deer were located an unequal number of times, I randomly selected 850 locations per deer across all seasons (Appendix 8). For each species, 10,000 random locations were obtained within a minimum convex polygon derived from all seasonal locations to represent availability of the whole landscape (Appendix 9). This resulted in a density of 3.8/km² and 3.7/km² available locations within the study area for mule and white-tailed deer respectively in each season. RSPF parameters were estimated with the ResourceSelection package in R (version 2.13.1, R Development Core Team 2011) using the logit link function and Nelder-Mead likelihood estimator, providing the following logistic equation:

$$S_j = \frac{\exp(\beta_0 + \beta_1 x_1 + \dots + \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 + \dots + \beta_p x_p)} \quad \text{eqn 3.1.}$$

where S_j is the probability of selection during season j with $B_0 \dots B_p$ estimated parameters and $x_0 \dots x_p$ are habitat covariates. Habitat covariates were chosen to reflect anthropogenic disturbance, predation risk, and food resources (see HABITAT COVARIATES), and were measured within 6 circular buffer sizes (120, 240, 500, 1000, 3000 and 5000 m radius). Covariates were not included in the same model if strongly correlated, based on Spearman's rank correlation ($r_s \geq 0.50$, $P < 0.05$). Competing models were ranked more conservatively using Bayesian Information Criterion (BIC) because it has a stricter parameter penalty

than AIC (Burnham & Anderson 2002). For source-sink habitat classification RSPF models were predicted across the study area at a 30-m pixel resolution using eqn 3.1.

RSPF Evaluation. RSPF models were evaluated for correspondence with deer use following Johnson et al. (2006) based on an independent set of locations from female VHF-collared deer (76 mule deer, 95 white-tailed deer) and GPS collars (9 mule deer, 6 white-tailed deer) withheld from the RSPF dataset. The RSPF values for the MCP encompassing the independent deer locations were grouped into 10 bins and the predicted proportion of locations within bin i was calculated using the area-weighted formula:

$$U_i = \frac{w_i A_i}{\sum_{j=1}^{10} w_j A_j} \quad \text{eqn 3.2.}$$

where w_i is the midpoint value with a range of RSPF values for bin i , A_i is the number of 30-m pixels of bin i and j is the total number of bins. Because in this analysis the locations across deer were not equal (2 – 5615 locations/deer), I calculated observed use as the mean proportion of locations across individuals occurring in each bin. The degree of correlation between the mean observed proportion and predicted proportions were assessed using Spearman's rank correlation assuming a monotonic relationship.

DEER SURVIVAL

Deer Mortalities. Mortalities among a total of 270 collared deer of both sexes (128 mule deer, 142 white-tailed deer) with VHF and GPS collars were

investigated within 24 hours of detecting a VHF mortality signal. The average length of time between signal detection and presumed time of mortality of 8.4 days (SD = 6.5). The kill location was considered the site of deer remains. Cause of death was classified as: hunter-harvest, vehicle collision, coyote predation, disease or unknown. I used cause-specific criteria to classify types of deaths that included detection of coyote tracks and scat, collar condition (i.e. cut or chewed), human garbage, boot tracks and tire markings (Woolsey 1985; Gauthier & Larsen 1986). If a cause could not be determined (28% of all mortalities) it was classified as unknown. Hunters reported harvested deer directly to Alberta Fish and Wildlife as part of the chronic wasting disease surveillance program and the herd reduction program. If no harvest location was provided (6 of 40 hunting mortalities) the last known location was considered the kill site. Any unknown death < 30 days post-capture (n = 2) was considered a capture myopathy (Beringer *et al.* 1996) and were censored, along with deer harvested during the herd reduction program (n = 6).

Annual Survival Rates. Annual survival rates were calculated for all causes of mortality using a Kaplan-Meier survival analysis (Therneau & Grambsch 2000; Therneau 2012). Data were pooled among years to create a recurrent year from 1 May to 30 April (Fieberg & DelGiudice 2009). Differences in survival rates between species and sex were evaluated with a score test after fitting a CPH because it can utilize left-censored data (Hosmer *et al.* 2008). The score test evaluates the likelihood of the null hypothesis that $\beta = 0$ (i.e. species has no effect

on survival rate) based on a null chi-squared distribution (Therneau & Grambsch 2000).

Cox Proportional Hazards Models. To determine the effects of habitat conditions on hunting and non-hunting (coyote, disease, vehicle collision and unknown) sources of mortality I derived independent CPH models (Cox 1972; Andersen & Gill 1982). I rarified the GPS and VHF locations to one location per day. Deer were censored if they were not located after > 29 days but were re-entered if relocated. Mortality dates were set as the mid-point between the date of the last known location and date of mortality detection, except where the mortality date was known with certainty (i.e. reported by hunter). I followed the approach of Therneau & Grambsch (2000) and divided time intervals into daily observations because they suggest it does not lead to bias in the parameters of time-dependent covariates of the CPH. I used a study-based time scale where time was measured continuously as the number of days since first deer capture (8 February 2006) because it did not require the modeling of complex temporal variation in mortality risk (Fieberg & DelGiudice 2009).

I used the COXPH function as part of the survival package (Therneau 2012) in R (version 2.13.1, R Development Core Team 2011), which uses the counting process formulation of Anderson and Gill (1982) and allows for left and right truncation as well as re-entry of individuals (Heisey & Fuller 1985). I used the CPH model:

$$\lambda_i = \lambda_o \exp(\sum_{j=1}^p \beta_j x_j) \quad \text{eqn 3.3.}$$

where λ is the i cause specific hazard rate, λ_0 is the base-line hazard rate, x is a habitat covariate and β an estimated parameter (Parmar *et al.* 1995). The regression was performed separately for hunting and non-hunting (Kalbfleisch & Prentice 2002; Putter *et al.* 2007), where non-hunting included mortalities of unknown cause. The unknown mortalities were assumed to be unrelated to hunting because their remains were never associated with any evidence of hunting mortality, and the majority of unknown mortalities (81%) occurred outside of the hunting season. I did not use a competing risk analysis with data augmentation (Lunn & McNeil 1995) because hunting and non-hunting mortality risk was not proportional. Also, separate analyses can provide nearly identical parameter estimates for the same dataset (Putter *et al.* 2007; Bakoyannis & Touloumi 2012) and allow more flexibility in differences in covariate inclusion. Proportionality assumption of the CPH model was tested using Schoenfeld residual plots and graphical methods (Therneau & Grambsch 2000; Cleves 2010).

For both hunting and non-hunting CPH models, I included species, sex and age, as well as their interactions with habitat covariates (see HABITAT COVARIATES). Deer age was categorized upon capture as either adult (≥ 24 months, 75% of captures) or yearlings (12 – 23 months, 13%) based on chest girth measurements and tooth eruption (Larson & Taber 1980). For a portion of deer (12%) classification as either adults or yearlings was uncertain; for this analysis they were assumed to be adults. Ages of yearlings were changed to adult on 3 June, which was the average reported mean parturition date for mule (Hamlin & Mackie 1989; Whittaker & Lindzey 1999; Johnstone-Yellin *et al.* 2006;

Johnstone-Yellin *et al.* 2009) and white-tailed deer (Verme 1977; DelGiudice *et al.* 1986; Whittaker & Lindzey 1999; Swanson *et al.* 2008). I evaluated non-linearity in the forms of the covariates using martingale residual plots (Therneau & Grambsch 2000; Cleves 2010).

Competing models were ranked based on Akaike information criterion adjusted for small sample size (AIC_c, Burnham & Anderson 2002), with sample size considered as the number of mortalities (Hosmer *et al.* 2008). Final models were evaluated by first summing the daily predicted risk for each deer and dividing by the number of days the deer was monitored, then calculating the area under the receiver operator curve (AUC, Fielding & Bell 1997) for mean daily risk between deer with observed mortalities versus those without using R 2.13.1 package ROCR (Sing *et al.* 2009). For source-sink habitat classification, CPH models were predicted across the study area at a 30-m pixel resolution using the exponential component of eqn 3.3.

PREGNANCY RATES

Pregnancy Data. Pregnancy rates were calculated based on female mule and white-tailed deer harvested during a winter herd reduction program for CWD in March of 2005-2007. The herd reduction program harvested all detected deer within a 10-km radius of previously known CWD positive cases using sharp shooters on the ground (2005 and 2006) and/or in helicopters (2007). For each deer the GPS location of the kill site and age based on tooth eruption and wear (Larson & Taber 1980) were recorded. I used only white-tailed deer harvested in

2005 when the number of fetuses per deer was recorded ($n = 325$). Because so few mule deer (32) were harvested in 2005, mule deer from all years (2005-2007) were included in the analysis ($n = 353$) but for these deer pregnant or not was recorded instead of the number of fetuses.

Summer Habitat Use Buffer. Habitat conditions surrounding the kill sites were measured within a circular buffer area of 6.74 km^2 for mule deer and 4.82 km^2 for white-tailed deer, reflecting the average size of their respective summer home ranges (E. Merrill unpublished data). However, because buffers around kill sites of deer harvested in late winter may not have reflected the actual area a deer used during the summer, I first evaluated how well the winter buffers reflected deer's summer use area using collared mule deer (VHF = 34, GPS = 14) and white-tailed deer (VHF = 49, GPS = 13). For each collared deer, I randomly selected a hypothetical harvest location among known locations in late winter (1 February – 31 March). Then placing varying buffer sizes ($0.1 - 25 \text{ km}^2$) around that location I calculated what proportion of locations in the previous summer (1 May – 30 November) were within that buffer to determine ability to reflect a summer use area.

Pregnancy Model. To quantify the habitat influence on reproduction, I modeled the pregnancy status of harvested females as a function of the landscape characteristics within a buffer surrounding each kill location using a logistic model:

$$P(x) = \frac{\exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)}{1 + \exp(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_p x_p)} \quad \text{eqn 3.4.}$$

where $x_1 \dots x_p$ include covariates for deer age (fawn or adult), habitat characteristics of the kill site and previous winter severity, and $\beta_0 \dots \beta_p$ are the estimated coefficients. Pregnancy status for white-tailed deer was set as ≥ 2 fetuses (1) or < 2 fetuses (0) because 77% of all white-tailed deer were pregnant, but for mule deer the status was denoted as pregnant (1) or not (0). Habitat covariates reflected food resources, predation risk and anthropogenic disturbance (see HABITAT COVARIATES). Competing models were ranked and evaluated based on small sample size AIC_c (Burnham & Anderson 2002). If the top ranked model lacked strong support (i.e. AIC_c weight $< 70\%$) then I model averaged those models constituting the top $> 95\%$ AIC_c weight (Anderson 2008). The final pregnancy models were evaluated using area under the receiver operator curve (Fielding & Bell 1997) using reclassified data. I assessed the spatial autocorrelation in model residuals by fitting a spline to the plotted correlogram with bootstrap confidence intervals (Cliff & Ord 1981; Bjornstad & Falck 2001). For source-sink habitat classification pregnancy models were predicted across the study area at a 30-m pixel resolution using equation 4.

SOURCE-SINK HABITAT

Fitness and Selection Correlation. Spatial correlation between the predictions of the fitness models (pregnancy, hunting and non-hunting) and the predictions of seasonal habitat selection were calculated from 1000 random locations in the study area using Spearman's ranks correlation. To help visualize the relationship

between fitness and selection, linear and loess smoothed lines were fit to the two plotted factors.

Mapping Source and Sink Habitat. RSPF values for females in summer, hunting season and all year were predicted across the study area (30-m pixels); the values were divided into ten ranked bins of equal area. At random 0.10 of the deer locations would therefore be expected within each bin. I therefore classified each bin into three habitat types based on the observed proportion of independent deer locations occurring in each bin using the following cut-offs: low selection < 0.10 , secondary = 0.10 and primary > 0.10 (Appendix 10). The independent deer locations were from the same VHF and GPS collared deer used to assess RSPF models (see above). The primary and secondary habitat classes were denoted as source where they overlapped the highest 50% of pregnancy fitness values and the lowest 50% of the hunting and non-hunting CPH values and designated as sink below or above these respective values. The 50% cut-off for the predicted pregnancy values represents a 0.91 probability of pregnancy for mule deer. As a result, the study area was divided into five habitat classes: unattractive, primary source, secondary source, primary sink and secondary sink.

Source-Sink, RSPF and Density. To evaluate whether adding fitness components explained deer density better than an RSPF alone, I used a Poisson generalized linear model (lme4 package in R, Bates *et al.* 2012) to relate winter deer densities (rounded to the nearest integer value) to the amount of source (both primary and secondary) habitat based on probability of pregnancy (1), hunting survival (2), non-hunting survival (3) or mean winter RSPF values (4) within square grid cells

of three sizes (25.3 km², 50.6 km² and 101.2 km²). These cell sizes were chosen because they were many times larger than a deer home range (25.3 km² cell 2-6x the size, 50.6km² is 4-11x and 101.2 km² is 8-22x, E. Merrill unpublished data). Competing models were ranked based on small sample size AIC_c (Burnham & Anderson 2002), with sample size equal to the number of unique grid cells at each grid scale (25.3 km² = 187 cells, 50.6km² = 103 cells and 101.2 km² = 53 cells). Deer densities were estimated from aerial population surveys from 2007 – 2009 (details below). A unique identifier for each cell was included as a random effect to account for repeated measures of density in different years. Because herd reductions were completed in the same area and time period (2005-2008), I included the number of deer culled within a cell in all previous years as a covariate to account for any reduction in density.

Deer population surveys were completed by experienced Alberta Fish and Wildlife crews using a helicopter covering pre-determined flight lines, which were either 400 or 1600 m apart representing 100% and 25% coverage respectively. Surveys were completed in January when trees lacked foliage and snow was typically present, which helped to maximize deer detectability. I did not correct for bias in deer sightability, but detection of deer in this study area was > 90% when snow was present (Habib *et al.* in press). I used surveyed data that covered the Canadian Forces Base Wainwright (WMU 728/730) in 2007 and 2009 as well as WMU 234 and 236 in 2008 and 2009. The Wainwright base and the study blocks within 234 and 236 were surveyed with 100% coverage while the remainder of 234 and 236 received 25% coverage. Only grid cells with > 20%

coverage were included in the analysis. The deer density D_i in grid cell i was estimated with the following equation:

$$D_i = \frac{C_i}{A_i} \quad \text{eqn 3.5.}$$

Where C_i is the number of deer detected within cell i and A_i is the area (km^2) surveyed within cell i . The area surveyed was determined by buffering the survey flight lines by 200 m.

HABITAT COVARIATES

RSPF Habitat Covariates. Anthropogenic disturbance including roads, linear features (roads, cut-lines, railroads and pipelines) and oil and gas wells with covariates measured both as the proximity to these features or the density within a buffer (Table 3.1). Habitat covariates which may increase or decrease predation risk included: proportion of forest and shrub cover, terrain ruggedness and slope, stream density and proximity and proximity or density of water bodies (lakes and ponds). For food resources I used the amount of agriculture or native grassland within a buffer. Also, the mean normalized difference vegetation index (NDVI), tassel cap greenness, shrub biomass, forb biomass, grass biomass, herbaceous biomass (sum of forb and grass) and total biomass (sum of shrub, forb and grass) within a buffer were used to index food resources. Where appropriate, I tested for covariate interactions with a binary covariate for near to the Battle River or Ribstone Creek (≤ 1 km) and evaluated non-linearity in habitat selection by including a 2nd order polynomial. All continuous covariates were standardized by

subtracting the mean and dividing by the standard error observed among the whole year dataset (Appendix 11). For details on spatial data used to calculate the habitat covariates see the SPATIAL HABITAT DATA section below.

CPH Habitat Covariates. The hunting CPH included habitat covariates for amount of cover (forest and shrubs), open habitat (agriculture and grassland) and terrain ruggedness in 3 different buffer sizes around each location. Buffer sizes corresponded with the mean minimum convex polygon encompassing daily movements by GPS-collared deer (0.4 km radius, SD = 0.5 km, n = 307), a small seasonal home range (1-km radius) and large seasonal home range (2-km radius, E. Merrill unpublished data). The smallest buffer is larger than the error associated with VHF telemetry locations and hunter reported kill sites. I also used distance to the nearest cover patch, town, road and linear features (roads, pipelines and seismic lines). To reflect areas with both hunter access (linear features) and deer vulnerability (open habitat) I created a covariate for the proportion of open habitat also within 0.3 km of a linear feature. Additionally, I included two indicator (0/1) covariates related to hunter access: location within provincial parks where hunting is illegal and location on public land, where hunters may have higher access compared to private land where permission to access is legally required.

For the non-hunting CPH models, I included the distance to water (ponds, lakes and rivers), terrain slope, terrain ruggedness and amount of cover to represent non-human predation risk. Exposure to forage was measured as a running mean of the current and all past locations since June 1 of the amount of:

forbs, grass, shrub and total biomass, NDVI, tassel cap greenness, proportion of agriculture and grassland all calculated within 400-m buffer around each location. The date of 1 June was chosen to represent the annual cycle of body condition in wild ungulates (Hewison *et al.* 1996; DelGiudice *et al.* 1992). To capture the importance of forest and shrub cover during the winter, I calculated a running mean of the proportion of forest, shrub and a combination of both within a 400-m buffer throughout winter (30 Nov – 30 April), with the mean value on the last day of winter held constant throughout the next summer to reflect the lingering effect of winter.

Pregnancy Habitat Covariates. Within the summer use buffer I measured the forage availability with a series of covariates including: average vegetation biomass by cover type, NDVI, tassel cap greenness and amount of agriculture. For average vegetation biomass I used separate covariates for shrub biomass, forb biomass, grass biomass, herbaceous biomass (sum of forb and grass) and total biomass (sum of shrub, forb and grass). To capture landscape factors, which would impact foraging efficiency via perceived predation risk (Lima 1998; Blanchard & Fritz 2007; Creel *et al.* 2007), I included: terrain ruggedness, amount of cover, road density, oil and gas well density, stream density and distance to town. Age was also included because pregnancy rates of adults are more robust to nutritional condition compared to fawns and yearlings (Verme 1969; Abler *et al.* 1976). Because an attempt was made to remove all deer in the vicinity, density (deer/km²) of other deer harvested during the herd reduction program was included as a covariate to account for potential resource competition negatively

impacting pregnancy rates (Coulson *et al.* 2000; Nicholson *et al.* 2006). Winter severity was calculated as the number of days with snow depths > 38cm and minimum temperatures < -17.7 °C from 1 November to 1 May (DelGiudice *et al.* 2002; Dawe 2011). Temperature and snow depth were collected by Environment Canada (2012), with measurements recorded in Lloydminster, Alberta which was on the Northern extent of the study area.

SPATIAL HABITAT DATA

Land Cover. Land cover proportions for forest, shrub, and both forest and shrub cover, agriculture and grasslands were derived with ETM+ multi-spectral imagery and Landsat 5 TM at a 30-m resolution (Agriculture and Agri-Food Canada 2010). Terrain slope and ruggedness were calculated using an 18-m resolution digital elevation model. Distance to well sites with an accuracy of ± 20 m was measured for active, abandoned and newly licensed oil and gas wells current as of 23 January 2006. All GIS layers were provided by Saskatchewan Environment, Spatial Data Warehouse Ltd. and Agriculture and Agri-Food Canada.

Vegetation Biomass. To determine grass, forb and shrub biomass, vegetation was sampled during 20-25 July in 174 transects, 25 or 50-m in length, in 2007 (59 transects) and 2008 (111 transects). In total, 12-25 sites were sampled in five vegetation communities (grassland, shrubland, forest, agriculture and wetland). Transects were sampled by clipping all forbs and grasses within 0.25 m² quadrats placed at 5-m intervals and visually estimating the proportion of clipped biomass that was the current annual growth. Vegetation clippings were dried at 50°C for

48 hours to obtain the dry weight. Dried weights were corrected by the proportion estimated to be the current annual growth, and averaged across sites within vegetation communities (Appendix 12).

Shrub biomass was estimated by first quantifying a basal diameter (BD) to biomass relationship for each shrub species following Visscher *et al.* (2006) from 6 to 30 individual stems collected in 2007. For each stem, BD was measured and the leaves and current annual growth (CAG) removed, and oven dried at 100 °C for 72 hours before weighing to the nearest 0.01 g. Biomass of stem CAG and leaves were then modeled separately for individual species as a function of BD using either linear or power relationships (Appendix 13). At each sample site, total number of stems for each shrub species was counted within 3 to 6 8-m² plots located at 10-m intervals along the transect and quantified the mean BD from 5 stems of representative size for each species. To determine species specific shrub biomass within plots, the average stem BD for each species was used to predict the average leaf and stem CAG biomass for each species and multiplied by the mean total number of stems within a plot. Shrub biomass estimates were averaged across plots to estimate the mean and standard deviation in grass, forb and shrub biomass along each transect. I then averaged shrub biomass across each vegetation community (Appendix 12). I assume that biomass values are proportional across community types throughout the year, because the regions habitat is open with forests having relatively open canopy cover.

Results

HABITAT SELECTION

According to the top RSPF models selected based on AIC ranking (Appendix 14), both deer species selected woody cover, with white-tailed deer selecting for intermediate areas of agriculture and areas with more fragmented cover patches reflected by edge density, and mule deer selecting for areas with a large extent native grassland and rugged terrain (Table 3.2, Appendix 15). White-tailed deer selected for rugged terrain only within 1 km of the Battle River or Ribstone Creek or during the hunting season. White-tailed deer avoided areas with high road densities during all times of the year and showed neither selection nor avoidance of well sites. In contrast, mule deer avoidance of anthropogenic areas varied seasonally with avoidance of roads only in winter and well sites in the summer and hunting season.

RSPF values of both species were strongly related ($r_s = 0.72$ to 1.00) to use of the landscape by an independent set of collared-deer (Table 3.3, Appendix 16). For both species-specific RSPF there was stronger correlation for the whole year and during winter than in summer or the hunting season.

DEER SURVIVAL

Cause-specific Mortalities. Deer were monitored an average of 428.3 ± 303.9 days (SD) per deer. There were 79 mortalities (38 white-tailed and 41 mule deer) including 40 that were attributed to hunter-harvest and 39 were non-hunting

related (26 unknown, 1 disease, 4 vehicle collision and 8 coyote). Hunting-related deaths comprised a higher proportion of mule deer (66%) than white-tailed deer (34%) mortalities (exact binomial test, $P < 0.01$) and especially males. Hunting deaths peaked in November, which corresponded with the rifle hunting season for deer (Fig. 3.1.A). Most coyote-related mortalities (75%) occurred during the winter months, while mortalities of unknown causes and vehicle collisions were distributed throughout the year except during the hunting season (Fig. 3.1.B).

Annual Survival Rates. Annual mule deer survival was 0.72 ± 0.04 (SE) and was no different than white-tailed deer (0.79 ± 0.03 , $P = 0.12$). However, males of both species had significantly lower survival (0.62 ± 0.07) compared to females (0.79 ± 0.02 , $P = 0.03$). Mule deer males had the lowest survival rate overall (0.52 ± 0.09 , Table 3.4), while the mule deer females and white-tailed deer of both sexes were relatively similar ($0.74 - 0.80$, $P < 0.01$). When annual survival rates were divided into hunting and non-hunting causes, white-tailed deer had higher survival from hunting than mule deer but the opposite was true for non-hunting (Fig. 3.2).

Cox Proportional Hazard Models. The top two models predicting the risk of mortality met proportional hazards assumptions based on Schoenfeld residuals goodness of fit test for hunting ($\chi^2 = 2.18$, $P = 0.90$) and non-hunting ($\chi^2 = 3.34$, $P = 0.50$). For the top ranked models there were no covariates that appeared both in the hunting and non-hunting models for either species (Table 3.5). In the top hunting model, male deer were more vulnerable to hunter-harvest than females (Table 3.6), were less likely to be harvested in a provincial park, and in areas with a high proportion of woody cover. White-tailed deer were most vulnerable to

hunting when on gentle slopes and mule deer on steep slopes. In the non-hunting but not the hunting model, yearlings were less likely to survive than adults. Deer that used native grasslands throughout the year and areas with more abundant forest cover in the winter were less likely to die from non-hunting mortality.

DEER REPRODUCTION

Pregnancy Rates. Adults of both species were much more likely to be pregnant than fawns (Table 3.7). A higher percentage of white-tailed deer fawns were pregnant (23%) than mule deer (8%, $X^2 = 7.46$, $df = 1$, $P = 0.01$), but there was no difference in adult pregnancy rates between the species ($X^2 = 0.0003$, $df = 1$, $P > 0.90$). Fourteen percent of adult mule deer had a litter of one and 86% had a litter size of two; no observations were made of triplets or greater (Appendix 17). In white-tailed deer, 16% of the adult females had litter sizes of one, 73% had twins, and 9% had triplets. One adult white-tailed deer had four fetuses and another had five. Adult mule deer had an average of 1.58 fetuses/female (SD = 0.76) while adult white-tailed deer had 1.71 fetuses/female (SD = 0.84) but this difference was not significant according to a Mann-Whitney rank sum test ($P = 0.46$).

Buffer Size for Summer Use Areas. For both species, resident deer had a greater proportion of their summer points within the hypothetical cull buffer than migrants (Fig. 3.3). For white-tailed deer buffers equal in size to a summer home range had $36.5\% \pm 5.1$ (SE) of summer locations for residents and $7.5\% \pm 5.0$ for migrators. A much greater portion of resident ($57.2\% \pm 6.0$) and migratory ($11.0\% \pm 8.9$) mule deer summer locations were present in an area the size of their

summer home range than for white-tailed deer. I used a buffer of 15.8 km² (2240-m radius) that encompassed 60% of locations of resident white-tailed deer because home range-sized buffer of white-tailed deer captured so few summer locations.

Pregnancy Models. For both species there was no evidence of significant spatial autocorrelation in the pregnancy model based on visual inspection of the spline fitted to the correlograms (Appendix 18). Age appeared in the top models for both species (Table 3.8). The odds of an adult mule deer being pregnant was 181x more than fawns but only 42x for white-tailed deer (e^{β} , Table 3.9). There was no detectable habitat influence on white-tailed deer pregnancy status. WSI in the previous winter reduced pregnancy rates among mule deer but I could not test for the effect WSI in white-tailed deer because data were available from only a single year. Mule deer were more likely to be pregnant in areas with rugged terrain and low well site density.

FITNESS AND SELECTION.

Habitat influenced the reproduction of mule deer only and based on the correlation between summer RSPF and pregnancy model (Table 3.10, Appendix 19) they selected for areas during the summer that increased their likelihood of becoming pregnant. In contrast, both species selected for habitats that improved their survival from natural and hunting mortality with mule deer showing a stronger selection for low risk areas than white-tailed deer.

SOURCES AND SINKS

Classification of Habitat Quality. For white-tailed deer 70% of the study area was classified as unattractive habitat for hunting and non-hunting mortality risk (Table 3.11). While for mule deer pregnancy and hunting habitat 60% was classified as unattractive but 70% of non-hunting was unattractive. Source habitat influencing pregnancy in mule deer was 2.4x more prevalent than sink habitat. The pregnancy source habitat was located along the Battle River and rugged portions of the Ribstone Creek near its intersection with the Battle River (Fig. 3.4). In contrast, the sink habitats for reproduction were located in the natural sand dune habitat (i.e. Wainwright dunes ecological reserve) where mule deer selected for areas associated with general terrain that reduced the likelihood of being pregnant.

The ratio of source habitat, where the risk of dying from non-hunting causes was low, to sink habitat was higher for mule deer (4.6x more source) than white-tailed deer (1.8x more source, Table 3.11). This was caused by mule deer selecting for native grassland, which increased non-hunting survival, but white-tailed deer did not. Additionally, white-tailed deer selected for woody cover (forest and shrubs) associated with agriculture which increased their risk because the woody cover associated with agriculture was typically shrubs, which unlike forest did not increase non-hunting survival. Non-hunting source habitats for mule deer were in areas with abundant forest and grassland (i.e. Wainwright dunes ecological reserve) while white-tailed deer had the same source habitat but more restricted to areas adjacent to agriculture (Fig. 3.5). Sink habitat for both species

were in shrub patches but white-tailed deer had additional sink within the small isolated shrub patches within the agricultural matrix.

In contrast, mule deer and white-tailed deer had proportionally similar amounts of source and sink habitat, 2.2x more source than sink, with respect to mortality risk from hunting, but these habitats had slightly different characteristics (Table 3.11). Both mule and white-tailed deer source habitat was associated with woody cover because it increased hunting survival (Fig. 3.5). However, white-tailed deer had more source habitat along the Battle River valley than mule deer because of the steep slopes increased white-tailed deer survival but decreased survival for mule deer. In addition, mule deer had more source habitat within parks than white-tailed deer, because white-tailed deer did not select strongly for the habitat within parks because they lacked sufficient agriculture. Both mule and white-tailed deer had sink habitat in more open areas with mule deer sink habitat on the steep slopes of the Battle River valley and white-tailed deer sinks in flat terrain generally within agricultural lands.

Deer Density and Habitat Quality. White-tailed deer densities across the three measurement scales averaged from 1.35-1.42 deer/km² (SD = 1.5-2.1) while mule deer averaged from 1.15-1.25 deer/km² (SD = 1.6-1.9). However, there was no difference in densities between the two species, across all scales, based on non-parametric Mann-Whitney U tests (P -value > 0.09, Appendix 20). Relationships between deer density and components of habitat quality were consistent across cells sizes so I present only the results for the analysis at a grid cell size of 25.3 km² (Table 3.12, Appendix 21). The number of deer harvested during the herd

reduction program in the previous winter was negatively related to density of deer in the area the following year (Appendix 22). For both species the proportion of source habitat (primary and secondary) in an area better predicted deer density than the average selection values for the area. However, for mule deer there was more support ($w_i \geq 0.92$) for the single-covariate model reflecting a positive relationship between mule deer density and amount of hunting source habitat (Table 3.12), while for white-tailed there was more support for a single-covariate model ($w_i \geq 0.99$) showing a positive relationship between deer density and the amount of non-hunting source habitat.

Mule deer multi-covariate models included pregnancy source combined with amount of hunting and non-hunting source respectively but hunting and non-hunting source habitat were strongly correlated at all three cell sizes (Spearman's rank correlation, $r_s \geq 0.86$). They were not included therefore in the same model. For white-tailed deer, amount of hunting and non-hunting source habitat were included in the same model at the 25.3 km² and 50.6 km² cell size but not at 101.2 km² because of a strong correlation ($r_s = 0.55$). The resulting multi-covariate models were no better than their single covariate counterparts for both species at all cell sizes, based on AIC_c rankings (Appendix 23).

Discussion

Source and sink habitats were not the same for the two deer species, in large part, due to differential habitat selection. In contrast to white-tailed deer, mule deer, selected for native grassland and rugged terrain across the study area

whereas white-tailed selected for areas of agriculture fragmented by cover and rugged areas adjacent to the Battle River and Ribstone Creek. Similar patterns have been reported for these species in Saskatchewan (Silbernagel *et al.* 2010), Texas (Brunjes *et al.* 2006) and Montana (Swenson *et al.* 1983). Further, areas predicted to have high selection values were positively correlated with use by an independent set of collared deer within the study area.

These species-specific selection patterns had consequences for the reproduction and, particularly for mortality of deer, that lead to identifying potential source-sink habitats in the study area. First, because I found no evidence of habitat features influencing the reproductive capacity of white-tailed deer, I could not map source habitats based on their reproduction potential. A lack of relationship may be related to the overall high reproductive capacity of white-tailed deer or more likely the summer buffer was too large (3x larger than an average white-tailed deer summer home range) to detect any relationship between habitat and pregnancy rates. In contrast, mule deer selected for areas of rugged terrain and low oil and gas well densities in summer, which I found increased their likelihood of being pregnant. It is unlikely that rugged terrain within the study area is of high forage value due to soil conditions (Sakai *et al.* 1995; Bochet & Garcia-Fayos 2004). Instead, mule deer may have select areas of low oil and gas well site density and rugged terrain due to reduced human disturbance (Sawyer *et al.* 2006; Sawyer *et al.* 2009) and lower vulnerability to coyote predation on rugged terrain (Lingle 2002) leading to less vigilance thus resulting in higher forage intake (Underwood 1982; Illius & Fitzgibbon 1994) and

pregnancy rates (Robinette *et al.* 1973; Tollefson *et al.* 2010). However, source habitat promoting pregnancy in mule deer was not related to their large-scale densities in winter. This may be because high pregnancy rates do not always result in high recruitment. In fact, Andelt *et al.* (2004) and Hurley *et al.* (2011) both found that mule deer recruitment was more dependent on juvenile survival than pregnancy rates, and annual variation in deer population size has been shown to be highly sensitive to juvenile survival (Gaillard *et al.* 2000; Gaillard *et al.* 2010). An alternative indicator, such as juvenile survival, may prove to be better at delineating reproductive sources and sinks than pregnancy rates, although these data are equally difficult to obtain.

My results do support that large-scale densities of deer were related to amount of source habitats that diminished the hazard for deer from natural and hunting mortality. Based on annual mortality rates, mule deer in the study area had higher rates of mortality from hunting than white-tailed deer (Fig. 3.2). This trend is not a product of the hunting regulations because mule deer harvest quotas are more restrictive than white-tailed deer (Alberta Government 2012; Saskatchewan Ministry of Environment 2012). Instead higher mortality rates in mule deer could be caused by hunter preference, similar to how preference for harvesting males increases their mortality risk compared to females (Nixon *et al.* 2001; Farmer *et al.* 2006). Alternatively, mule deer-specific behaviours like being conspicuous and tolerant of human presence (Kramer 1973; Geist 1981) and their tendency to stop and look back when pursued by hunters (O'Connor & Goodwin 1961; Geist 1998) could make them easier to harvest. Both mechanisms, hunter

preference and greater vulnerability, are consistent with higher hunter success rates for mule deer (~60-70%) compared to white-tailed deer (~30-50%) throughout the study region (Dave Moore Personal Communications).

Despite a higher harvest risk for mule deer during the hunting season, mule deer did not select for less risky habitat than white-tailed deer. During the hunting season both species selected for woody cover that provided security from hunters (Nixon *et al.* 1991; Brinkman *et al.* 2004), which reduced their mortality hazard. However, a species interaction with slope in the CPH indicated that white-tailed deer were at greater risk on gentle terrain, while mule deer had more risk on steep slopes. Increased mortality of white-tailed deer on gentle terrain may occur because they encounter more hunters as there is 2x higher road density in gentle than steep terrain (Appendix 24) and when hunters leave the road they tend to remain on gentle terrain due to ease of mobility (Stedman *et al.* 2004). In comparison, I did not expect to find that mule deer had a greater risk of being killed by a hunter on steep slopes because mule deer run faster on steep slopes than on flat terrain (Lingle 1992; Lingle 1993), which should improve their odds of escaping hunters. But Farmer *et al.* (2006), also found that Sitka deer (*Odocoileus hemionus sitkensis*) in Alaska had higher hunting mortality risk on steep slopes, attributing this fact to hunters having a better line of sight on slopes.

In contrast to hunting mortality, white-tailed deer had a higher non-hunting annual mortality rate than mule deer because they selected for agricultural areas, whose cumulative exposure reduced deer survival. While mule selected for grasslands, which increased their survival. This may be related to forage

availability, because while forage biomass was lower in grasslands than agricultural areas in the summer (Appendix 12), grasslands are not harvested prior to winter. As a result grasslands can act as an over-winter forage resource at a time when food is most limited and critical to deer survival (DePerno *et al.* 2000; Bender *et al.* 2007; Bishop *et al.* 2009). White-tailed deer also selected for areas with mixed woody cover-agriculture habitat, with the woody cover typically shrubland rather than forest. Based on cumulative mortality risk, use of forest but not shrublands improved survival. Aspen forest habitat may provide more effective shelter from wind and reduce snow depths (E. Merrill, unpublished data). Consequently, white-tailed deer selection patterns indicate higher non-hunting mortality than mule deer, which may explain why white-tailed deer densities related best to the amount of non-hunting source habitat.

Inclusion of fitness components into habitat assessments may help to improve the understanding of ecological processes and their influence on animal distributions. For example, mule deer have long been known to select for rugged terrain (Kufeld *et al.* 1988; Lingle 2002; Stewart *et al.* 2002), but it has not been realized that selection of rugged terrain may make them more vulnerable to hunters and thus reduce local population densities. By relating fitness components to density, one may be able to better understand the relative importance of certain habitats at limiting animal densities. For example, Heppell *et al.* (1996) showed the benefits of a program to increase hatchling survival for endangered sea turtles (*Lepidochelys kempi*) were minimal because adult survival was more important to the population. Similarly, I found evidence that habitat which improved

pregnancy rates in this region had little effect on deer densities compared to habitat which influenced adult survival. These findings have implications for local managers with goals of reducing deer densities for disease control (Langenberg *et al.* 2008; Wasserberg *et al.* 2009) because targeting habitat which impacts deer survival would be more effective than focusing on pregnancy. Additionally, understanding how different habitats influence deer survival and reproduction may help to inform future spatially explicit CWD spread models, as survival and recruitment are known to influence CWD transmission and prevalence (Potapov *et al.* 2012).

Table 3.1. Habitat covariates used in the RSPF, hunting (H.CPH) and non-hunting (N.CPH) survival and pregnancy (Preg) models calculated for mule and white-tailed deer in east-central Alberta from 2006-2010. For covariates measured within a circular buffer the buffer size was denoted by a subscript following the end of the covariate name (i.e. Cover_{400m}).

Covariate	Model	Description
Dtown	H.CPH, Preg	Distance (km) to nearest town, village or hamlet.
Dlinear	H.CPH, RSPF	Distance (km) to nearest linear feature (road, cutline or pipeline).
Linear_open	H.CPH	Proportion of open land cover (agriculture and grassland) also within 300 m of a linear feature (road, cutline or pipeline) within circular buffers of 3 sizes: 400 m , 1 km, and 2 km radius.
Park	H.CPH	Assigned a 1 if inside either Wainwright dunes ecological reserve or Dillberry provincial parks where hunting is illegal, otherwise assigned a 0.
Public land	H.CPH	Assigned a 1 if inside grazing lease or rangelands heritage park, otherwise a 0.
Dcover	H.CPH	Distance (km) to nearest shrub or forest cover.
Cover	All models	Proportion of shrub and forest cover within a circular buffer (buffer size depends on model with details in text).
Rugged	All models	Standard deviation in elevation (m) within a circular buffer.
Slope	H.CPH, N.CPH, RSPF	Slope (%) for an individual cell within a 3 x 3 cell window
Droad	H.CPH, N.CPH, RSPF	Distance (km) to nearest road.
D_water	N.CPH, RSPF	Distance (km) to nearest lake, pond and river.
M.Agriculture	N.CPH	Running mean of amount of agriculture measured as the proportion within a circular buffer with a 400m radius. Reset to zero on June 1.
M.NDVI	N.CPH	Running mean of the average NDVI value within a circular buffer with a 400m radius. Reset to zero on June 1.
M.greeness	N.CPH	Running mean of the average tassel cap greeness value within a circular buffer with a 400m radius. Reset to zero on June 1.

Table 3.1. Continued

Covariate	Model	Description
M.total.biomass	N.CPH	Running mean of shrub, forb and grass biomass (g/m^2) within a circular buffer with a 400m radius. Reset to zero on June 1.
M.shrub.biomass	N.CPH	Running mean of shrub biomass (g/m^2) within a circular buffer with a 400m radius. Reset to zero on June 1.
M.forb.biomass	N.CPH	Running mean of forb biomass (g/m^2) within a circular buffer with a 400m radius. Reset to zero on June 1.
M.grass.biomass	N.CPH	Running mean of grass biomass (g/m^2) within a circular buffer with a 400m radius. Reset to zero on June 1.
M.herb.biomass	N.CPH	Running mean of herb biomass (g/m^2 , grasses plus forbs) within a circular buffer with a 400m radius. Reset to zero on June 1.
M.grassland	N.CPH	Running mean of grass biomass (g/m^2) within a circular buffer with a 400m radius. Reset to zero on June 1.
M.cover.winter	N.CPH	Running mean of proportion of cover (forest and shrubs) within a circular buffer with a 400m radius during the winter (30 Nov – 30 April). In summer the covariate is equal to the running mean from the previous winter then reset to zero on first day of winter.
M.shrub.winter	N.CPH	Running mean of proportion of shrub cover within a circular buffer with a 400m radius during the winter (30 Nov – 30 April). In summer the covariate is equal to the running mean from the previous winter then reset to zero on first day of winter.
M.forest.winter	N.CPH	Running mean of proportion of forest cover within a circular buffer with a 400m radius during the winter (30 Nov – 30 April). In summer the covariate is equal to the running mean from the previous winter then reset to zero on first day of winter.
M.forest.winter	N.CPH	Running mean of proportion of forest cover within a circular buffer with a 400m radius during the winter (30 Nov – 30 April). In summer the covariate is equal to the running mean from the previous winter then reset to zero on first day of winter.
NDVI	Preg	Mean NDVI value within a circular buffer.

Table 3.1. Continued

Covariate	Model	Description
Greenness	Preg	Mean tassel cap greenness value within a circular buffer.
Total.biomass	Preg	Mean of total biomass (shrub, forb and grass, g/m ²) within a circular buffer.
Shrub.biomass	Preg	Mean of shrub biomass (g/m ²) within a circular buffer.
Forb.biomass	Preg	Mean of forb biomass (g/m ²) within a circular buffer.
Grass.biomass	Preg	Mean of grass biomass (g/m ²) within a circular buffer.
Herb.biomass	Preg	Mean of herb biomass (forb and grass, g/m ²) within a circular buffer.
WSI	Preg	Winter severity index measured as the number of days with snow depths > 38cm and minimum temperatures <17.7 °C from 1 November to 1 May.
Well	Preg, RSPF	Number of oil and gas wells per km ² within a set buffer.
Dwell	RSPF	Distance (km) to nearest oil and gas well.
Road	Preg, RSPF	Length of roads (km) per km ² within a set buffer.
Linear	RSPF	Length of stream linear feature (road, cutline or pipeline, km) per km ² within a set circular buffer.
Density	Preg	Number of deer harvested during the herd reduction program per km ² within a set buffer.
Stream	Preg, RSPF	Length of stream (km) per km ² within a set circular buffer.
Grass	RSPF, Preg	Proportion of native grassland within a circular buffer.
Dstream	RSPF	Distance (km) to nearest stream.
Water	RSPF	Assigned a 1 if inside a pond or lake otherwise equal to 0.
Edge	Preg, RSPF	Length of cover edge per km ² within a set circular buffer.
Agri	RSPF, Preg	Proportion of agriculture within a circular buffer.
River	RSPF	Assigned a value of 1 within 1km of the Battle River or Ribstone Creek, otherwise equal to 0.
Species	H.CPH, N.CPH	Mule deer are assigned a value of 1 and white-tailed deer a value of 0.
Sex	H.CPH, N.CPH	Males are assigned a value of 1 and females a value of 0.

Table 3.1. Continued

Covariate	Model	Description
Age	Preg, H.CPH, N.CPH	Age is a binary covariate where adult is equal to 1 and fawns and yearlings are equal to 0.

Table 3.2. Coefficients (β) of the RSPFs for mule deer (MUDE) and white-tailed deer (WTDE) for the whole year, summer and hunting season and their respective standard errors (SE). Covariate descriptions provided in Table 3.1. Winter RSPF coefficients are reported in Appendix 15.

Species	Covariates	Whole Year		Summer		Hunting Season	
		β	SE	β	SE	β	SE
MUDE	Intercept	4.71	0.10	-1.91	0.03	-2.39	0.09
	Cover _{1km}	3.77	0.05	0.72	0.01	0.53	0.01
	Grass _{500m}	2.52	0.04	0.32	0.01	0.16	0.01
	Rugged _{500m}	0.13	0.01	0.91	0.11	0.70	0.03
	Water	-2.03	0.13	-1.57	0.01	-1.65	0.10
	Stream _{1km}	0.68	0.02	0.76	0.02	0.72	0.01
	Road _{500m}	-0.09	0.01	0.08	0.01	0.04	0.01
	Well _{1km}	-0.03	0.01	-0.20	0.01	-0.21	0.01
WTDE	Intercept	-4.85	0.20	-8.86	0.11	-6.63	0.15
	Cover _{120m}	2.14	0.09	0.97	0.01	0.89	0.02
	Edge _{1km}	0.08	0.01	0.01	0.01	0.07	0.02
	Agri _{5km}	18.44	0.94	34.92	0.52	26.37	0.76
	Agri _{5km} ²	-18.73	1.03	-37.34	0.58	-26.92	0.80
	Rugged _{500m}	-0.04	0.01	-0.05	0.02	0.03	0.03
	Stream _{1km}	0.02	0.02	0.31	0.01	0.39	0.02
	Water	-0.72	0.08	-0.33	0.05	-0.64	0.06
	Road _{1km}	-0.43	0.03	-0.29	0.01	-0.27	0.02
	Rugged _{500m} x River	0.10	0.01	1.32	0.09	1.22	0.10

Table 3.3. Spearman's rank correlation (r_s) between predicted habitat use by mule deer and white-tailed deer based on a seasonal RSPF derived from GPS-collared deer and expected habitat use based on proportions of VHF locations within each of 10-area weighted bins.

Species	Season	r_s	P
Mule deer	Whole Year	0.95	<0.01
	Summer	0.85	<0.01
	Winter	0.96	<0.01
	Hunting Season	0.78	0.01
White-tailed deer	Whole Year	1.00	<0.01
	Summer	0.72	0.02
	Winter	0.98	<0.01
	Hunting Season	0.72	0.02

Table 3.4. Annual survival rates for mule deer and white-tailed deer of each sex observed among 270 GPS and VHF collared deer monitored from 8 February 2006 to 27 February 2010 in east-central Alberta. Reported are the standard error (SE) and 95% confidence interval (CI) of the estimated survival rate and number of deer in each analysis (n).

Species	Sex	Survival	SE	95% CI	n
Mule deer	Male	0.52	0.09	0.36 – 0.74	43
	Female	0.74	0.09	0.58 – 0.94	85
White-tailed deer	Male	0.77	0.04	0.70 – 0.85	41
	Female	0.80	0.03	0.73 – 0.86	101

Table 3.5. The top ranked Cox proportional hazard (CPH) models for hunting and non-hunting mortality of mule deer and white-tailed deer in east-central Alberta. Presented are number of model parameters (k), Akaike's information criterion corrected for small sample size (AIC_c), AIC difference (ΔAIC_c), AIC_c weight (w_i) and area under the receiver operator curve (AUC). Covariate descriptions are provided in Table 3.1.

Mortality	Covariates	k	AIC_c	ΔAIC_c	w_i	AUC
Hunting	Sex, Cover _{400m} , Park, Slope, Slope x Species	6	798.3	0.0	0.74	0.62
	Species, Sex, Cover _{400m} , Park, Slope, Slope x Species	7	801.3	3.0	0.18	0.60
	Species, Sex, Cover _{400m} , Park	5	803.2	4.9	0.06	0.62
	Species, Sex, Park	4	805.1	6.8	0.02	0.62
	Null model	1	820.2	21.9	<0.01	-
Non-Hunting	Age, M.forest.winter, M.grassland	4	796.5	0.0	0.56	0.64
	M.forest.winter, M.grassland	3	798.7	2.2	0.18	0.60
	Age, M.forest.winter	3	799.2	2.7	0.15	0.58
	Age, M.grassland	3	800.1	3.6	0.09	0.65
	Null model	1	803.0	12.9	0.02	-

Table 3.6. Coefficients (β) of the Cox proportional hazards models for hunting and non-hunting sources of mortality of white-tailed and mule deer and their respective standard errors (SE). Negative coefficient indicates reduced hazard. Covariate descriptions provided in Table 3.1.

Mortality Type	Covariates	β	Exp(β)	SE	<i>P</i> -value
Hunting	Slope	-0.60	0.55	0.21	< 0.01
	Sex (male = 1)	1.06	2.89	0.37	< 0.01
	Cover _{400m}	-1.21	0.30	0.62	0.05
	Park (inside = 1)	-17.07	<0.0005	0.59	< 0.01
	Slope x Species	0.65	1.92	0.21	< 0.01
Non-Hunting	Age (Adult = 1)	-1.62	0.20	0.62	0.02
	M.forest.winter	-5.18	0.006	3.18	0.10
	M.grassland	-1.73	0.18	0.82	0.03

Table 3.7. Pregnancy rates among mule and white-tailed deer from 2005-2007 harvested during the herd reduction program in east-central Alberta.

Species		Fawn		Adult	
		No.	Percent	No.	Percent
Mule deer	Pregnant	7	7.9	246	93.2
	Not Pregnant	82	92.1	18	6.8
	Total	89	100	264	100
White-tailed deer	Pregnant	43	23.2	584	92.4
	Not Pregnant	142	76.8	48	7.6
	Total	185	100	632	100

Table 3.8. The null and the top-ranked models for predicting the probability of pregnancy status for winter culled mule deer (pregnant; not pregnant) and white-tailed deer (< 2 fetuses; ≥ 2 fetuses) harvested in east-central Alberta. Presented are number of model parameters (k), Akaike's information criterion corrected for small sample size (AIC_c), AIC difference (ΔAIC_c), AIC_c weight (w_i) and area under the receiver operator curve (AUC). Covariate descriptions are provided in Table 3.1.

Species	Covariates	k	AIC_c	ΔAIC_c	w_i	AUC
Mule deer	Age, WSI, Rugged, Well	5	183.3	0.0	0.30	0.92
	Age, WSI, Rugged	4	183.4	0.1	0.28	0.91
	Age, WSI	3	183.6	0.3	0.26	0.91
	Age	2	184.5	1.2	0.16	0.89
	Null model	1	422.8	239.5	<0.01	0.50
White-tailed deer	Age	2	324.4	0.0	0.99	0.80
	Null model	1	446.8	122.4	<0.01	0.50

Table 3.9. Coefficients (β) of the logistic models predicting the probability of a mule deer being pregnant and for white-tailed deer the probability of having ≥ 2 fetuses and their respective standard errors (SE) and 95% confidence intervals (CI). Covariate descriptions provided in Table 3.1.

Species	Covariates	β	SE	95% CI
Mule deer	Intercept	-1.20	1.16	-3.48, 1.07
	Age (adult = 1)	5.20	0.49	4.34, 6.16
	WSI	-0.06	0.03	-0.13, 0.004
	Rugged	0.10	0.06	-0.03, 0.22
	Well	-0.08	0.05	-0.19, 0.02
White-tailed deer	Intercept	-2.72	0.46	-3.62, -1.82
	Age	3.73	0.48	2.79, 4.67

Table 3.10. Spearman rank correlation coefficient (r_s) between seasonal selection for areas by mule deer (MUDE) and white-tailed deer (WTDE) and the predicted values of the probability of being pregnant and the relative risk of dying from hunting or non-hunting mortality based on fitness models described in the text. Correlations are based on values at 1000 random locations across the study area.

Fitness Model	Habitat Selection	Species	r_s	P -value
Pregnancy	Summer RSPF	Mule deer	0.55	<0.01
Hunting CPH	Hunting Season RSPF	Mule deer	-0.41	<0.01
		White-tailed deer	-0.31	<0.01
Non-Hunting CPH	All Year RSPF	Mule deer	-0.61	<0.01
		White-tailed deer	-0.40	<0.01

Table 3.11. Percentage of the five habitat classes within the 13,268 km² study area for white-tailed deer (WTDE) and mule deer (MUDE) specific to the combination of pregnancy rates with summer selection, hunting mortality risk with hunting season selection, and non-hunting mortality risk with selection throughout the year.

Habitat Type	Species	Unattractive (%)	Source (%)			Sink (%)		
			1°	2°	Total	1°	2°	Total
Pregnancy	MUDE	60.0	22.1	6.0	28.1	8.0	3.9	11.9
Hunting	MUDE	60.0	21.9	5.7	27.6	7.9	4.5	12.4
	WTDE	70.0	15.0	5.7	20.7	5.0	4.3	9.3
Non-Hunting	MUDE	70.0	17.5	7.1	24.6	2.4	3.0	5.4
	WTDE	70.0	13.6	5.6	19.2	6.4	4.4	10.8

Table 3.12. Top ranked Poisson model of deer density at a 25.3 km² scale as a function of proportion of primary and secondary source habitat for increasing the likelihood of pregnancy, reducing the risk of hunting and non-hunting mortality, or the mean winter RSPF for mule deer (MUDE) and white-tailed deer (WTDE). All models, including the null model, include covariates for the number of deer harvested during the herd reduction program and a random effect of grid cell over time. Presented are number of model parameters (k), Akaike's information criterion corrected for small sample size (AIC_c), AIC difference (ΔAIC_c), AIC_c weight (w_i). Models at two other scales (50.6 and 101.2 km²) provide similar results described in Appendix 21.

Species	Model	k	AIC_c	ΔAIC_c
Mule deer	Hunting source	4	459.6	0.0
	Non-hunting source	4	464.4	4.7
	$RSPF_{winter}$	4	479.7	20.1
	Pregnancy source	4	513.9	54.2
	Null model	3	515.4	55.8
White-tailed deer	Non-hunting source	4	445.5	0.0
	$RSPF_{winter}$	4	475.6	30.1
	Hunting source	4	485.7	40.2
	Null model	3	511.4	65.9

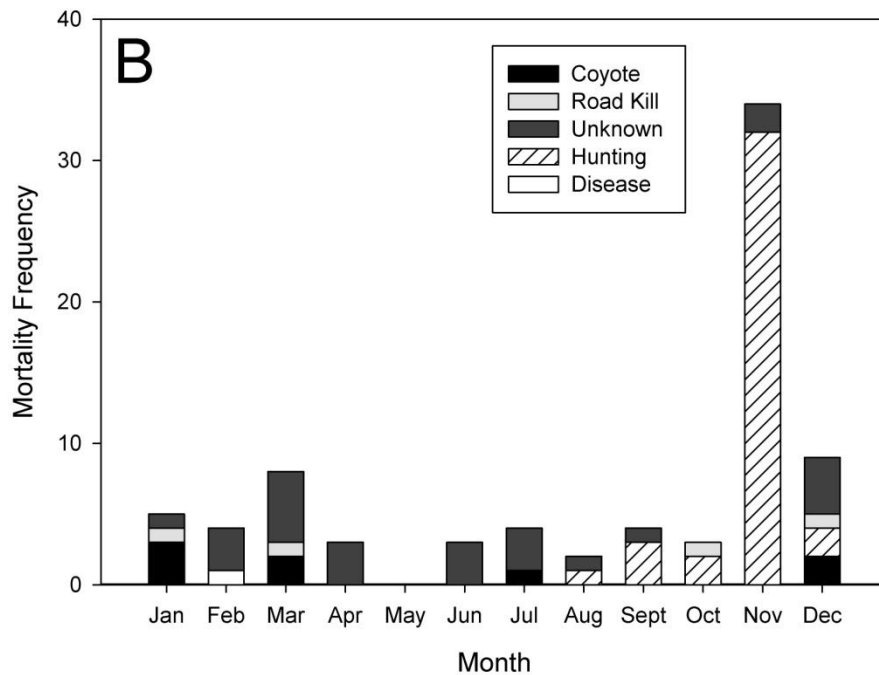
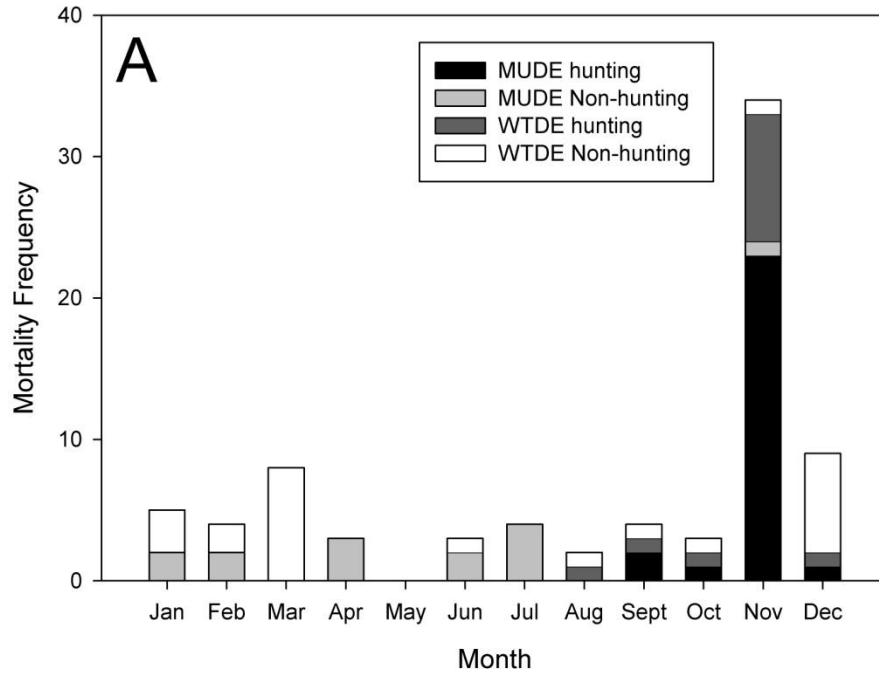


Fig. 3.1. A) Number of hunting and non-hunting mortalities observed in each month for mule (MUDE) and white-tailed deer (WTDE). Deaths were observed among 270 collared deer monitored between 2006 and 2009 in east-central Alberta. B) Hunting and non-hunting mortalities with non-hunting divided into its component causes including: vehicle collisions, disease, coyote predation and unknown causes.

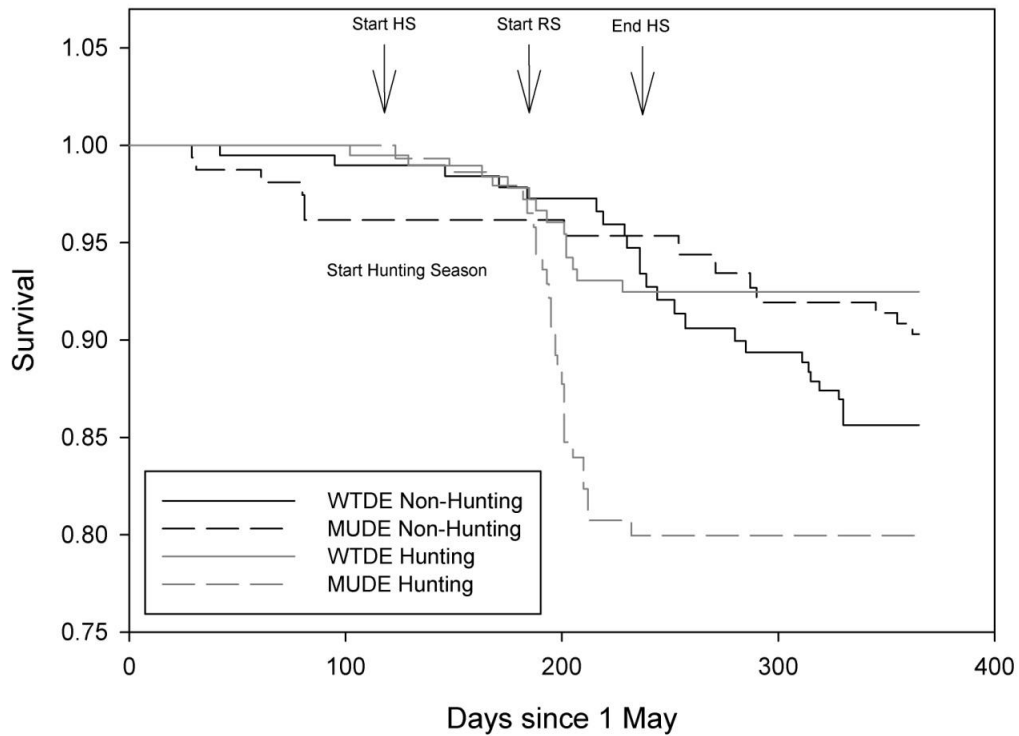


Fig. 3.2. Survival function for hunting and non hunting mortality events observed among 270 mule deer (MUDE) and white-tailed deer (WTDE) monitored in east-central Alberta. For each mortality type, the functions were estimated using a Kaplan-Meier survival analysis while mortality events from alternative risks are censored. Survival data across years was combined into a recurrent year (1 May to 30 April, Fieberg & Delgiudice 2009). Indicated are the start of the hunting season (HS) and the rifle season (RS) as well as the end of the hunting season.

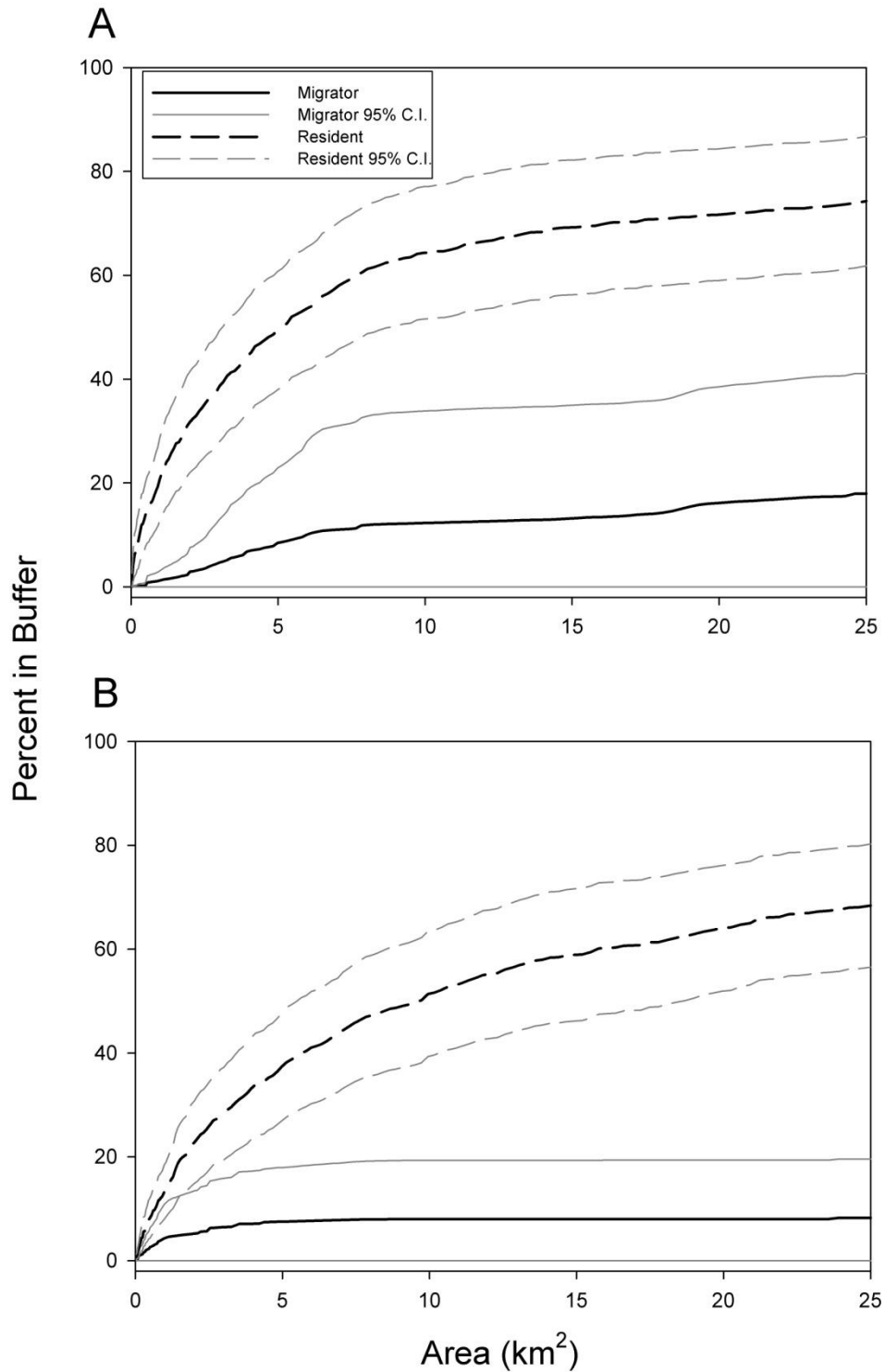


Fig. 3.3. Percentage of summer locations (1 May to 30 November) within a hypothetical buffer centered on a randomly selected location in late winter (1 February to 31 March) averaged across VHF and GPS collared female mule (A, n = 48) white-tailed deer (B, n = 62).

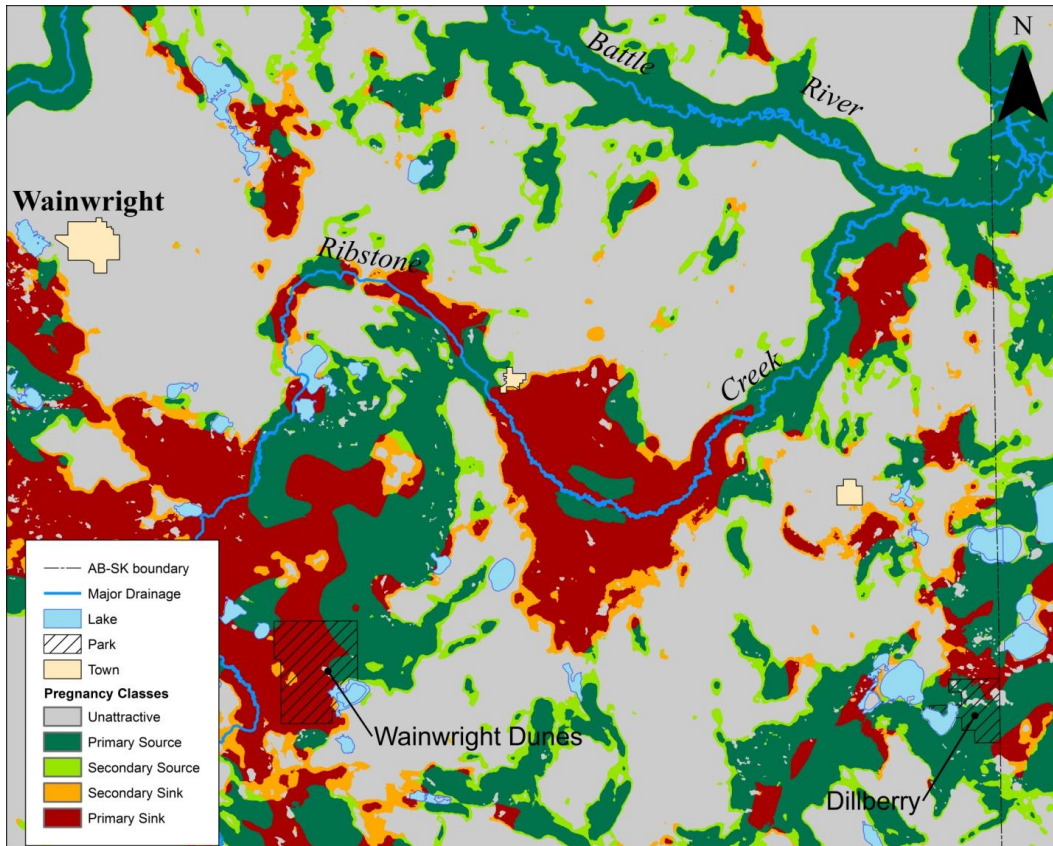


Fig. 3.4. Pregnancy habitat classes including: unattractive, source (primary and secondary) and sink (primary and secondary) for mule deer in east-central Alberta.

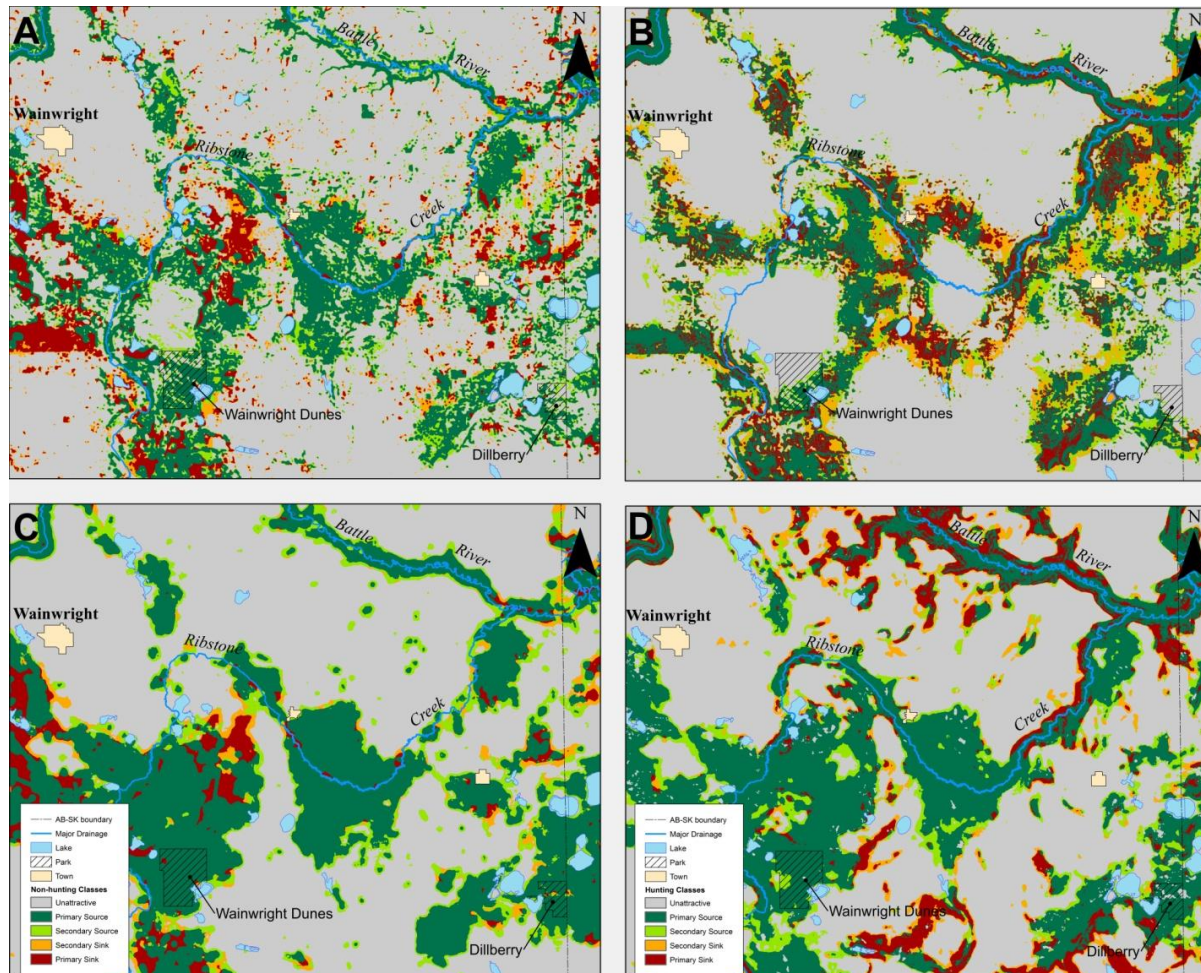


Fig. 3.5. Hunting (B; D) and non-hunting (A; C) mortality habitat classes including: unattractive, source (primary and secondary) and sink (primary and secondary) for white-tailed deer (A; B) and mule deer (C; D) in east-central Alberta.

Literature Cited

- Abler, W., Buckland, D., Kirkpatrick, R. & Scanlon, P. (1976) Plasma progesterone and puberty in fawns as influenced by energy and protein. *Journal of Wildlife Management*, **40**, 442-446.
- Acton, D.F., Padbury, G.A. & Stushnoff, C.T. (1998) *The Ecoregions of Saskatchewan*, Regina, Sask, University of Regina, Canadian Plains Research Center.
- Agriculture and Agri-Food Canada. (2010) Land Cover for Agricultural Regions of Canada circa 2000. <http://www4.agr.gc.ca/AAFC-AAC/display-afficher.do?id=1227733122679&lang=eng> [Accessed 12 May 2010]
- Alberta Government. (2012) Alberta guide hunting regulations 2012. <http://albertaregulations.ca/huntingregs/> [Accessed 1 September 2012]
- Aldridge, C.L. & Boyce, M.S. (2007) Linking occurrence and fitness to persistence: Habitat-based approach for endangered greater sage-grouse. *Ecological Applications*, **17**, 508-526.
- Allombert, S., Gaston, A. & Martin, J. (2005) A natural experiment on the impact of overabundant deer on songbird populations RID E-5059-2010. *Biological Conservation*, **126**, 1-13.
- Andelt, W., Pojar, T. & Johnson, L. (2004) Long-term trends in mule deer pregnancy and fetal rates in Colorado. *Journal of Wildlife Management*, **68**, 542-549.
- Andersen, P.K. & Gill, R.D. (1982) Cox regression-model for counting-processes - a large sample study. *Annals of Statistics*, **10**, 1100-1120.
- Anderson, D.R. (2008) *Model Based Inference in the Life Sciences: A Primer on Evidence*, New York, Springer.
- Arlt, D. & Part, T. (2007) Nonideal breeding habitat selection: A mismatch between preference and fitness. *Ecology*, **88**, 792-801.
- Bakoyannis, G. & Touloumi, G. (2012) Practical methods for competing risks data: A review. *Statistical Methods in Medical Research*, **21**, 257-272.
- Barrett, M.W., Nolan, J.W. & Roy, L.D. (1982) Evaluation of a hand-held net-gun to capture large mammals. *Wildlife Society Bulletin*, **10**, 108-114.
- Bates, D., Maechler, M. & Bolker, B. (2012) lme4: Linear mixed-effects models using Eigen and Eigen. *R Package Version 0.999999-0*, .

- Bender, L.C., Lomas, L.A. & Browning, J. (2007) Condition, survival, and cause-specific mortality of adult female mule deer in north-central new mexico. *Journal of Wildlife Management*, **71**, 1118-1124.
- Beringer, J., Hansen, L., Wilding, W., Fischer, J. & Sheriff, S. (1996) Factors affecting capture myopathy in white-tailed deer. *Journal of Wildlife Management*, **60**, 373-380.
- Bird, R.D. (1961) Ecology of the aspen parkland of western canada in relation to land use. *Canada Department of Agriculture, Ottawa, Ontario, Canada*.
- Bishop, C.J., White, G.C., Freddy, D.J., Watkins, B.E. & Stephenson, T.R. (2009) Effect of enhanced nutrition on mule deer population rate of change. *Wildlife Monographs*, **172**, 1-28.
- Bjornstad, O. & Falck, W. (2001) Nonparametric spatial covariance functions: Estimation and testing. *Environmental and Ecological Statistics*, **8**, 53-70.
- Blanchard, P. & Fritz, H. (2007) Induced or routine vigilance while foraging. *Oikos*, **116**, 1603-1608.
- Bochet, E. & Garcia-Fayos, P. (2004) Factors controlling vegetation establishment and water erosion on motorway slopes in valencia, spain. *Restoration Ecology*, **12**, 166-174.
- Bock, C. & Jones, Z. (2004) Avian habitat evaluation: Should counting birds count? *Frontiers in Ecology and the Environment*, **2**, 403-410.
- Bowyer, R.T. & Kie, J.G. (2009) Thermal landscapes and resource selection by black-tailed deer: Implications for large herbivores. *California Fish and Game*, **95**, 128-139.
- Brinkman, T.J., Jenks, J.A., DePerno, C.S., Haroldson, B.S. & Osborn, R.G. (2004) Survival of white-tailed deer in an intensively farmed region of minnesota. *Wildlife Society Bulletin*, **32**, 726-731.
- Brunjes, K.J., Ballard, W.B., Humphrey, M.H., Harwell, F., McIntyre, N.E., Krausman, P.R. & Wallace, M.C. (2006) Habitat use by sympatric mule and white-tailed deer in texas. *Journal of Wildlife Management*, **70**, 1351-1359.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*, 2nd edn. New York, Springer.

- Chang, K.T., Verbyla, D.L. & Yeo, J.J. (1995) Spatial-analysis of habitat selection by sitka black-tailed deer in southeast alaska, usa. *Environmental Management*, **19**, 579-589.
- Cleves, M.A. (2010) *An Introduction to Survival Analysis using Stata*, 3rd edn. College Station, Tex, Stata Press.
- Cliff, A.D. & Ord, J.K. (1981) *Spatial Processes: Models & Applications*, London, Pion.
- Clover, M.R. (1954) A portable deer trap and catch-net. *California Fish and Game*, **40**, 367-373.
- Cook, J., Johnson, B., Cook, R., Riggs, R., Delcurto, T., Bryant, L. & Irwin, L. (2004) Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildlife Monographs*, **155**, 1-61.
- Coulson, T., Milner-Gulland, E. & Clutton-Brock, T. (2000) The relative roles of density and climatic variation on population dynamics and fecundity rates in three contrasting ungulate species. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **267**, 1771-1779.
- Cox, D.R. (1972) Regression models and life-tables. *Journal of the Royal Statistical Society Series B-Statistical Methodology*, **34**, 187-&.
- Creel, S., Christianson, D., Liley, S. & Winnie, J.A., Jr. (2007) Predation risk affects reproductive physiology and demography of elk. *Science*, **315**, 960-960.
- Dawe, K. (2011) *Factors driving range expansion of white-tailed deer, odocoileus virginianus, in the boreal forest of northern alberta, canada*. Ph.D., University of Alberta.
- DelGiudice, G., Mech, L., Paul, W. & Karns, P. (1986) Effects on fawn survival of multiple immobilizations of captive pregnant white-tailed deer. *Journal of Wildlife Diseases*, **22**, 245-248.
- DelGiudice, G., Mech, L., Kunkel, K., Gese, E. & Seal, U. (1992) Seasonal patterns of weight, hematology, and serum characteristics of free-ranging female white-tailed deer in minnesota. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **70**, 974-983.
- DelGiudice, G., Riggs, M., Joly, P. & Pan, W. (2002) Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central minnesota. *Journal of Wildlife Management*, **66**, 698-717.

- Delgiudice, G.D., Fieberg, J., Riggs, M.R., Carstensen Powell, M. & Pan, W. (2006) A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management*, **70**, 1556-1568.
- Delibes, M., Gaona, P. & Ferreras, P. (2001) Effects of an attractive sink leading into maladaptive habitat selection. *American Naturalist*, **158**, 277-285.
- DePerno, C.S., Jenks, J.A., Griffin, S.L. & Rice, L.A. (2000) Female survival rates in a declining white-tailed deer population. *Wildlife Society Bulletin*, **28**, 1030-1037.
- DePerno, C., Jenks, J. & Griffin, S. (2003) Multidimensional cover characteristics: Is variation in habitat selection related to white-tailed deer sexual segregation? RID B-7321-2009. *Journal of Mammalogy*, **84**, 1316-1329.
- Dias, P.C. (1996) Sources and sinks in population biology. *Trends in Ecology & Evolution*, **11**, 326-330.
- Environment Canada. (2012) National climate data and information archive. [Http://climate.Weatheroffice.Gc.ca/climateData/canada_e.html](http://climate.Weatheroffice.Gc.ca/climateData/canada_e.html), [Accessed 1 August 2012]
- Environment Canada. (2011) Canadian climate normals or averages 1971-2000. http://www.climate.weatheroffice.gc.ca/climate_normals/index_e.html [Accessed 5 August 2012]
- Falcucci, A., Ciucci, P., Maiorano, L., Gentile, L. & Boitani, L. (2009) Assessing habitat quality for conservation using an integrated occurrence-mortality model RID C-7677-2009 RID A-8637-2008. *Journal of Applied Ecology*, **46**, 600-609.
- Farmer, C.J., Person, D.K. & Bowyer, R.T. (2006) Risk factors and mortality of black-tailed deer in a managed forest landscape. *Journal of Wildlife Management*, **70**, 1403-1415.
- Fieberg, J. & DelGiudice, G.D. (2009) What time is it? choice of time origin and scale in extended proportional hazards models. *Ecology*, **90**, 1687-1697.
- Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation*, **24**, 38-49.
- Fletcher, R.J., Jr., Orrock, J.L. & Robertson, B.A. (2012) How the type of anthropogenic change alters the consequences of ecological traps. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 2546-2552.

- Frair, J.L., Merrill, E.H., Allen, J.R. & Boyce, M.S. (2007) Know thy enemy: Experience affects elk translocation success in risky landscapes. *Journal of Wildlife Management*, **71**, 541-554.
- Fretwell, S.D. & Lucas Jr, H.L. (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor*, **19**, 16-36.
- Gaillard, J., Coulson, T. & Festa-Bianchet, M. (2010) Demographic processes: Lessons from long-term, individual-based studies. *Dynamics of Large Herbivore Populations in Changing Environments : Towards Appropriate Models* Anonymous pp. 98-116. Chichester, West Sussex, UK; Hoboken, NJ, Wiley-Blackwell.
- Gaillard, J., Festa-Bianchet, M., Yoccoz, N., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367-393.
- Gauthier, D.A. & Larsen, D.G. (1986) *Predator Identification at Moose Calf Mortality Sites, Southwest Yukon*, Whitehorse, YK, Yukon Renewable Resources.
- Geist, V. (1998) *Deer of the World : Their Evolution, Behaviour, and Ecology*, 1st edn. Mechanicsburg, PA, Stackpole Books.
- Geist, V. (1981) Behavior: Adaptive strategies in mule deer. *Mule and Black-Tailed Deer of North America* (ed O. Wallmo), pp. 605. Lincoln, Nebraska, University of Nebraska Press.
- Gilroy, J.J., Anderson, G.Q.A., Vickery, J.A., Grice, P.V. & Sutherland, W.J. (2011) Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Animal Conservation*, **14**, 620-629.
- Gratson, M.W. & Whitman, C. (2000) Characteristics of idaho elk hunters relative to road access on public lands. *Wildlife Society Bulletin*, **28**, 1016-1022.
- Griffin, P.C. & Mills, L.S. (2009) Sinks without borders: Snowshoe hare dynamics in a complex landscape. *Oikos*, **118**, 1487-1498.
- Grovenburg, T.W., Swanson, C.C., Jacques, C.N., Deperno, C.S., Klaver, R.W. & Jenks, J.A. (2011) Female white-tailed deer survival across ecoregions in minnesota and south dakota. *American Midland Naturalist*, **165**, 426-435.
- Guisan, A. & Thuiller, W. (2005) Predicting species distribution: Offering more than simple habitat models. *Ecology Letters*, **8**, 993-1009.

- Habib, T.J., Moore, D.A., & Merrill, E.H. (in press) Detection and stratification approaches for aerial surveys of deer in prairie-parklands. *Wildlife Research*, in press.
- Hamlin, K.L. & Mackie, R. (1989) *Mule deer in the missouri river breaks, montana: A study of population dynamics in a fluctuating environment*. Montana Department of Fish, Wildlife and Parks.
- Hansen, L. (2011) Extensive management. *Biology and Management of White-Tailed Deer* (ed D. Hewitt G.), pp. 409-451. Boca Raton, FL, CRC Press.
- Harden, C., Woolf, A. & Roseberry, J. (2005) Influence of exurban development on hunting opportunity, hunter distribution, and harvest efficiency of white-tailed deer. *Wildlife Society Bulletin*, **33**, 233-242.
- Hebblewhite, M. (2006) *Linking predation risk and forage to ungulate population dynamics*. PhD, University of Alberta.
- Heinrichs, J.A., Bender, D.J., Gummer, D.L. & Schumaker, N.H. (2010) Assessing critical habitat: Evaluating the relative contribution of habitats to population persistence. *Biological Conservation*, **143**, 2229-2237.
- Heisey, D. & Fuller, T. (1985) Evaluation of survival and cause-specific mortality-rates using telemetry data. *Journal of Wildlife Management*, **49**, 668-674.
- Heppell, S., Crowder, L. & Crouse, D. (1996) Models to evaluate headstarting as a management tool for long-lived turtles. *Ecological Applications*, **6**, 556-565.
- Hewison, A., Angibault, J., Boutin, J., Bideau, E., Vincent, J. & Sempere, A. (1996) Annual variation in body composition of roe deer (*capreolus capreolus*) in moderate environmental conditions. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **74**, 245-253.
- Hollander, F.A., Van Dyck, H., Martin, G.S. & Titeux, N. (2011) Maladaptive habitat selection of a migratory passerine bird in a human-modified landscape. *Plos One*, **6**, e25703.
- Horner, M.A. & Powell, R.A. (1990) Internal structure of home ranges of black bears and analyses of home-range overlap. *Journal of Mammalogy*, **71**, 402-410.
- Hosmer, D.W., Lemeshow, S. & May, S. (2008) *Applied Survival Analysis : Regression Modeling of Time-to-Event Data*, 2nd edn. Hoboken, N.J, Wiley-Interscience.

- Hurley, M.A., Unsworth, J.W., Zager, P., Hebblewhite, M., Garton, E.O., Montgomery, D.M., Skalski, J.R. & Maycock, C.L. (2011) Demographic response of mule deer to experimental reduction of coyotes and mountain lions in southeastern Idaho. *Wildlife Monographs*, **178**, 1-33.
- Illius, A.W. & Fitzgibbon, C. (1994) Costs of vigilance in foraging ungulates. *Animal Behaviour*, **47**, 481-484.
- Jensen, R.A., Wisz, M.S. & Madsen, J. (2008) Prioritizing refuge sites for migratory geese to alleviate conflicts with agriculture. *Biological Conservation*, **141**, 1806-1818.
- Johnson, C., Nielsen, S., Merrill, E., McDonald, T. & Boyce, M. (2006) Resource selection functions based on use-availability data: Theoretical motivation and evaluation methods. *Journal of Wildlife Management*, **70**, 347-357.
- Johnstone-Yellin, T.L., Shipley, L.A., Myers, W.L. & Robinson, H.S. (2009) To twin or not to twin? trade-offs in litter size and fawn survival in mule deer. *Journal of Mammalogy*, **90**, 453-460.
- Johnstone-Yellin, T., Shipley, L. & Myers, W. (2006) Effectiveness of vaginal implant transmitters for locating neonatal mule deer fawns. *Wildlife Society Bulletin*, **34**, 338-344.
- Jones, M.D. & Pelton, M.R. (2003) Female American black bear use of managed forest and agricultural lands in coastal North Carolina. *Ursus (Knoxville)*, **14**, 188-197.
- Kalbfleisch, J.D. & Prentice, R.L. (2002) *The Statistical Analysis of Failure Time Data*, 2nd edn. Hoboken, N.J, J. Wiley.
- Kauhala, K. & Tiilikainen, T. (2002) Radio location error and the estimates of home-range size, movements, and habitat use: A simple field test. *Annales Zoologici Fennici*, **39**, 317-324.
- Kie, J. & Bowyer, R. (1999) Sexual segregation in white-tailed deer: Density-dependent changes in use of space, habitat selection, and dietary niche. *Journal of Mammalogy*, **80**, 1004-1020.
- Killmaster, C.H., Osborn, D.A., Warren, R.J. & Miller, K.V. (2007) Deer and understory plant responses to a large-scale herd reduction on a Georgia state park. *Natural Areas Journal*, **27**, 161-168.
- Knight, T.M., Dunn, J.L., Smith, L.A., Davis, J. & Kalisz, S. (2009) Deer facilitate invasive plant success in a Pennsylvania forest understory. *Natural Areas Journal*, **29**, 110-116.

- Kolbe, J. & Janzen, F. (2002) Impact of nest-site selection on nest success and nest temperature in natural and disturbed habitats. *Ecology*, **83**, 269-281.
- Kramer, A. (1973) Interspecific behaviour and dispersion of two sympatric deer species. *The Journal of Wildlife Management*, **37**, 288-300.
- Kufeld, R.C., Bowden, D.C. & Schrupp, D.L. (1988) Habitat selection and activity patterns of female mule deer in the front-range, colorado. *Journal of Range Management*, **41**.
- Langenberg, J.A., Miller, M.W. & Creekmore, L. (2008) *Alberta Chronic Wasting Disease Management Program Review Panel Report*.
<http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/documents/AlbertaCWDManagement-ProgramReviewPanelReport-Feb2008.pdf>
- Larson, J.S. & Taber, R.D. (1980) Criteria of sex and age. *Wildlife Management Techniques Manual* (ed S.D. Schemnitz), pp. 143-202. Washington, D.C., The Wildlife Society.
- Lele, S.R. (2009) A new method for estimation of resource selection probability function. *Journal of Wildlife Management*, **73**, 122-127.
- Lele, S.R. & Keim, J.L. (2006) Weighted distributions and estimation of resource selection probability functions. *Ecology*, **87**, 3021-3028.
- Lima, S. (1998) Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Stress and Behavior*, **27**, 215-290.
- Lingle, S. (2002) Coyote predation and habitat segregation of white-tailed deer and mule deer. *Ecology*, **83**, 2037-2048.
- Lingle, S. (1993) Escape gaits of white-tailed deer, mule deer, and their hybrids - body configuration, biomechanics, and function. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **71**, 708-724.
- Lingle, S. (1992) Escape gaits of white-tailed deer, mule deer and their hybrids - gaits observed and patterns of limb coordination. *Behaviour*, **122**, 153-181.
- Lishawa, S.C., Bergdahl, D.R. & Costa, S.D. (2007) Winter conditions in eastern hemlock and mixed-hardwood deer wintering areas of vermont. *Canadian Journal of Forest Research-Revue Canadienne De Recherche Forestiere*, **37**, 697-703.

- Lunn, M. & McNeil, N. (1995) Applying cox regression to competing risks. *Biometrics*, **51**, 524-532.
- McArdle, B.H., Gaston, K.J. & Lawton, J.H. (1990) Variation in the size of animal populations - patterns, problems and artifacts. *Journal of Animal Ecology*, **59**, 439-454.
- Mitchell, B., Mccowan, D. & Nicholson, I.A. (1976) Annual cycles of body-weight and condition in scottish-red deer, cervus-elaphus. *Journal of Zoology*, **180**, 107-127.
- Morrison, M. (2001) Invited paper: A proposed research emphasis to overcome the limits of wildlife-habitat relationship studies. *Journal of Wildlife Management*, **65**, 613-623.
- Morris, D.W. (2003) Toward an ecological synthesis: A case for habitat selection. *Oecologia*, **136**.
- Morris, D.W. (2011) Adaptation and habitat selection in the eco-evolutionary process. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 2401-2411.
- Naves, J., Wiegand, T., Revilla, E. & Delibes, M. (2003) Endangered species constrained by natural and human factors: The case of brown bears in northern spain. *Conservation Biology*, **17**, 1276-1289.
- Nicholson, M., Bowyer, R. & Kie, J. (2006) Forage selection by mule deer: Does niche breadth increase with population density? *Journal of Zoology*, **269**, 39-49.
- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in alberta. *Biological Conservation*, **130**, 217-229.
- Nixon, C.M., Hansen, L.P., BREWER, P.A., CHELSVIG, J.E., Esker, T.L., Etter, D.R., Sullivan, J.B., Koerkenmeier, R. & Mankin, P.C. (2001) Survival of white-tailed deer in intensively farmed areas of illinois. *Canadian Journal of Zoology*, **79**, 581-588.
- Nixon, C., Hansen, L., Brewer, P. & Chelsvig, J. (1991) Ecology of white-tailed deer in an intensively farmed region of illinois. *Wildlife Monographs*, **118**, 3-77.
- O'Connor, J. & Goodwin, G.G. (1961) *The Big Game Animals of North America. with Natural Histories by George G. Goodwin. Full Color Paintings and*

Black and White Drawings by Douglas Allen, Scientific Animal Portraits by Alexander Seidel, New York, Outdoor life.

- Parmar, M.K.B., Machin, D. & Uabard. (1995) *Survival Analysis : A Practical Approach*, Chichester; Toronto, J. Wiley.
- Pauley, G.R., Peek, J.M. & Zager, P. (1993) Predicting white-tailed deer habitat use in northern idaho. *Journal of Wildlife Management*, **57**, 904-913.
- Potapov, A., Merrill, E. & Lewis, M.A. (2012) Wildlife disease elimination and density dependence. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 3139-3145.
- Pulliam, H. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652-661.
- Putter, H., Fiocco, M. & Geskus, R.B. (2007) Tutorial in biostatistics: Competing risks and multi-state models. *Statistics in Medicine*, **26**, 2389-2430.
- Qi, D., Zhang, S., Zhang, Z., Hu, Y., Yang, X., Wang, H. & Wei, F. (2012) Measures of giant panda habitat selection across multiple spatial scales for species conservation. *Journal of Wildlife Management*, **76**, 1092-1100.
- R Development Core Team. (2011) *R: A Language and Environment for Statistical Computing*, Vienna, Austria, R Foundation for Statistical Computing.
- Robinette, W.L., Baer, C.H., Pillmore, R.E. & Knittle, C.E. (1973) Effects of nutritional change on captive mule deer. *Journal of Wildlife Management*, **37**, 312-326.
- Sakai, A., Ohsawa, T. & Ohsawa, M. (1995) Adaptive significance of sprouting of euptelea-polyandra, a deciduous tree growing on steep slopes with shallow soil. *Journal of Plant Research*, **108**, 377-386.
- Saskatchewan Ministry of Environment. (2012) Programs and services - hunting. <http://www.environment.gov.sk.ca/hunting>. [Accessed 1 September 2012]
- Sawyer, H., Nielson, R., Lindzey, F. & McDonald, L. (2006) Winter habitat selection of mule deer before and during development of a natural gas field. *Journal of Wildlife Management*, **70**, 396-403.
- Sawyer, H., Kauffman, M.J. & Nielson, R.M. (2009) Influence of well pad activity on winter habitat selection patterns of mule deer. *Journal of Wildlife Management*, **73**, 1052-1061.

- Silbernagel, E. (2010) *Factors affecting the movement patterns of mule deer (odocoileus hemionus) in southern saskatchewan: Implications for chronic wasting disease spread*. M.Sc., University of Saskatchewan, Saskatoon, Saskatchewan.
- Sing, T., Sander, O., Beerenwinkel, N. & Lengauer, T. (2009) ROCR: Visualizing the performance of scoring classifiers. *R Package Version 1.0-4*, .
- Smallwood, K.S. & Schonewald, C. (1998) Study design and interpretation of mammalian carnivore density estimates. *Oecologia*, **113**, 474-491.
- Stedman, R., Diefenbach, D.R., Swope, C.B., Finley, J.C., Luloff, A.E., Zinn, H.C., San Julian, G.J. & Wang, G.A. (2004) Integrating wildlife and human-dimensions research methods to study hunters. *Journal of Wildlife Management*, **68**, 762-773.
- Stewart, K., Bowyer, R., Kie, J., Cimon, N. & Johnson, B. (2002) Temporospatial distributions of elk, mule deer, and cattle: Resource partitioning and competitive displacement. *Journal of Mammalogy*, **83**, 229-244.
- Storlie, J.T. (2006) *Movements and habitat use of female roosevelt elk in relation to human disturbance on the hoko and dickey game management units, washington*. Master of Science, Humboldt State University, California, USA.
- Storm, D.J., Nielsen, C.K., Schaubert, E.M. & Woolf, A. (2007) Space use and survival of white-tailed deer in an exurban landscape. *Journal of Wildlife Management*, **71**, 1170-1176.
- Swanson, C.C., Jenks, J.A., DePerno, C.S., Klaver, R.W., Osborn, R.G. & Tardiff, J.A. (2008) Does the use of vaginal-implant transmitters affect neonate survival rate of white-tailed deer *odocoileus virginianus*? *Wildlife Biology*, **14**, 272-279.
- Swenson, J.E., Knapp, S.J. & Wentland, H.J. (1983) Winter distribution and habitat use by mule deer and white-tailed deer in southeastern montana. *Prairie Naturalist*, **15**, 97-112.
- Swihart, R., Weeks, H., Easter-Pilcher, A. & DeNicola, A. (1998) Nutritional condition and fertility of white-tailed deer (*odocoileus virginianus*) from areas with contrasting histories of hunting. *Canadian Journal of Zoology- Revue Canadienne De Zoologie*, **76**, 1932-1941.
- Telfer, E.S. (1970) Winter habitat selection by moose and white-tailed deer. *Journal of Wildlife Management*, **34**, 553-576.

- Therneau, T.M. (2012) A package for survival analysis in S. R package version 2.36-12.
- Therneau, T.M. & Grambsch, P.M. (2000) *Modeling Survival Data: Extending the Cox Model*, New York, Springer.
- Tollefson, T.N., Shipley, L.A., Myers, W.L., Keisler, D.H. & Dasgupta, N. (2010) Influence of summer and autumn nutrition on body condition and reproduction in lactating mule deer. *Journal of Wildlife Management*, **74**, 974-986.
- Underwood, R. (1982) Vigilance behavior in grazing african antelopes. *Behaviour*, **79**, 81-107.
- Van Horne, B. (1983) Density as a misleading indicator of habitat quality. *Journal of Wildlife Management*, **47**, 893-901.
- Verme, L. (1977) Assessment of natal mortality in upper michigan deer. *Journal of Wildlife Management*, **41**, 700-708.
- Verme, L. (1969) Reproductive patterns of white-tailed deer related to nutritional plane. *Journal of Wildlife Management*, **33**, 881-887.
- Visscher, D., Merrill, E., Fortin, D. & Frair, J. (2006) Estimating woody browse availability for ungulates at increasing snow depths. *Forest Ecology and Management*, **222**, 348-354.
- Walter, W.D., Leslie, D.M., Jr. & Jenks, J.A. (2006) Response of rocky mountain elk (*cervus elaphus*) to wind-power development. *American Midland Naturalist*, **156**, 363-375.
- Wasserberg, G., Osnas, E.E., Rolley, R.E. & Samuel, M.D. (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.
- Whittaker, D. & Lindzey, F. (1999) Effect of coyote predation on early fawn survival in sympatric deer species. *Wildlife Society Bulletin*, **27**, 256-262.
- Woolsey, N.C. (1985) Coyote field guide. *Arizona Game and Fish Department Special Report*, **15**, 1-39.

CHAPTER 4

CONCLUSIONS AND MANGEMENT IMPLICATIONS

Conclusions

In this thesis I addressed two aspects of deer spatial ecology that may contribute to the spread of CWD in mule and white-tailed deer in east-central Alberta. First, I built a CWD model that predicted disease risk based on local habitat characteristics, deer species and sex, and connectivity to previously detected CWD-positive cases. Similar to reports elsewhere in the prairie provinces of Canada (Rees *et al.* 2012), deer harvested from an area were more likely to be CWD infected if they were mule deer, male and killed in habitat associated with the river valleys and agriculture. Unlike in southern Saskatchewan, I found that not only were agricultural areas associated with river drainages at high risk of CWD, but also areas associated with roads away from rivers that had high connectivity to previous CWD-positives. Rees *et al.* (2012) found that proximity to major rivers increased risk but not small creeks, while I showed that areas with high stream density, whether river or creek, were at high risk.

My study is also among the first to quantify the influence of landscape heterogeneity on deer movement and to use this information to predict the risk of CWD introduction into uninfected areas (see also Garlick *et al.* 2011). Several studies suggest that deer movement is an important component to the spread of CWD (Conner & Miller 2004; Blanchong *et al.* 2008; Frost *et al.* 2009; Clements *et al.* 2011). However, I identified for the first time that landscape connectivity

based on deer movement responses is a better predictor of the likelihood of a deer harvested from an area being CWD-positive than Euclidian distance, although similar work has been done for livestock (Gilbert *et al.* 2005) and human disease (Meyers *et al.* 2005; Remais *et al.* 2010). My results suggest that more realism is needed to represent the potential for CWD introduction (Joly *et al.* 2006; Rees *et al.* 2012). CWD spread risk models need to be based on local deer ecology, which has been suggested by Remais *et al.* (2010) for disease models in general.

In using the risk model, I was able to pro-actively assess and identify areas that should be prioritized for surveillance and control prior to disease detection. My approach to risk assessment was novel because risk estimates for a wildlife management unit (WMU) were based not only on landscape attributes (Farnsworth *et al.* 2005; Joly *et al.* 2006; Rees *et al.* 2012), but also on species and sex composition. I found that including the deer herd composition was important to disease risk based on artificially adjusting the herd composition in each WMU, and demonstrating that a hypothetical all male mule deer population had significantly higher CWD risk than an all female white-tailed deer population.

Second, I classified source-sink habitat based on deer selection, reproduction and survival to determine which type of source habitat best predicted deer densities as an initial step in modeling CWD spread. This is the first application of a fitness-based approach to modeling habitat of mule and white-tailed deer or of a game species that I am aware of. The two species had different source-sink habitats in part because of variation in habitat selection with mule deer densities better relating to hunting and white-tailed deer natural mortality

risk. Habitat selection has also been shown to be an important determinate of lifetime reproductive success in red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) when reproductive output has been tracked for a generation or more (McLoughlin *et al.* 2006; Mcloughlin *et al.* 2007). I was the first to evaluate if source-sink habitat, based on the Nielsen *et al.* (2006) approach, better predicted habitat quality than selection alone by comparing the source-sinks to winter deer densities, with the assumption that deer would congregate in higher quality habitat in the winter conforming to an ideal free distribution (Fretwell & Lucas 1970). The fact that survival was most important to spatial variation in deer densities is consistent with the generalization that adult survival is the limiting factor in most ungulate populations (Gaillard *et al.* 2000; Gaillard *et al.* 2010). If these sources and sinks have a significant effect on the dynamics of CWD transmission, then identifying them is an important first step in developing spatially explicit models of disease spread.

Management Implications

My results offer several insights for management of CWD in Alberta. First, the fact that mule deer connectivity better explained CWD occurrence on the landscape than connectivity based on white-tailed deer movements supports the hypothesis that mule deer in the prairie provinces of Canada may be the main initial driver of CWD introduction into new areas (Rees *et al.* 2012). This has implications for CWD management in regions where the two species are sympatric and mule deer have higher prevalence (Miller *et al.* 2000; Conner *et al.* 2007; Osnas *et al.* 2009). It has been suggested that the removal of juvenile deer

would help slow CWD spread (Cullingham *et al.* 2011) because of their high dispersal rate (Dobson 1982; Nixon *et al.* 1994). Such a program should preferentially target mule deer rather than white-tailed deer.

The pattern of CWD risk varied throughout the study area with the southern portion having a concentration of high risk near the river drainages (i.e. Battle River and Ribstone Creek), while in the northern portion risky areas were more diffuse. This has implications for the type of management strategy applied to these two regions. I would suggest that in the South managers should institute targeted deer removal in the high risk areas along the rivers with a professional sharp-shooter, similar to the herd reduction program (Pybus 2012), assuming it becomes an option in the future. I expect this approach to be most effective because for other pathogens prioritizing highest risk areas for disease control has been shown to improve the likelihood of reducing disease spread and eliminating the disease (Tildesley *et al.* 2009; Beest *et al.* 2011). However, because the risky habitat is less concentrated in the North targeted deer removals may not be feasible in terms of economics and/or logistics. Therefore I would suggest focusing on reducing deer densities throughout the region by increasing hunter-harvest.

Sink habitats would be expected to have lower CWD transmission rates compared to source habitat for several reasons. First, a generally low, non-disease related survival rate in sink habitat reduces individual longevity and increases population turn-over with faster turn-over creating less opportunity for the pathogen to be transmitted from infected to healthy individuals thus reducing the

probably of disease persistence (Pongsumpun *et al.* 2008; Bellan 2010; Rascalou *et al.* 2012). Longevity of infected deer may be particularly important for a disease like CWD due to the accumulation of CWD prions in the environment (Johnson *et al.* 2006), which is probably an important means of transmission (Miller *et al.* 2004; Miller *et al.* 2006; Almberg *et al.* 2011), because even asymptomatic deer can shed prions through feces over a long time period (7-11 months, Tamgueney *et al.* 2009).

Second, Potapov *et al.* (2012) showed that increased recruitment of juveniles can have a dilution effect on overall CWD prevalence because vertical transmission rates are low (Gross & Miller 2001; Miller & Williams 2003) and there is an infusion of new healthy individuals. Reproductive sources could also have a disproportionate influence on spread because of their high production of juveniles, because juvenile males are likely to be infected (Miller *et al.* 2000; Conner *et al.* 2007; Osnas *et al.* 2009) and disperse great distances (Dobson 1982; Diefenbach *et al.* 2008), as far as 40 km in this study, with their arrival in new regions increasing the likelihood of CWD establishment (Gross & Miller 2001). Higher densities in source habitat could increase the number of dispersers leaving the source via density dependent dispersal (Matthysen 2005). However, even if dispersal is not density dependent, as observed in several deer populations (Shaw *et al.* 2006; Long *et al.* 2008; Loe *et al.* 2009), a source can still produce a higher numbers of dispersers relative to a sink because assuming a constant dispersal rate if source habitat produced 2x more juveniles than sink the result would be 2x more dispersers leaving the source. Therefore source habitat, because of high

survival and reproduction, has the potential to contribute more to the spread and persistence of CWD than sink habitat. As a result, managers may choose to focus their control efforts on sources rather than sinks and future CWD spread models may need to incorporate source-sink effects.

Future Directions

The CWD risk model I have provided can serve as an important management tool for controlling the spread of CWD by allowing managers to identify areas where CWD is likely to occur before it can be detected so that the disease can be removed prior to establishment. A quick response to CWD introduction is critical because it is very difficult to eradicate once it has become locally established (Williams & Miller 2003; Miller *et al.* 2004; Langenberg *et al.* 2008), due in part to the accumulation of prions in the environment that continue to infect naive deer long after the death of infected individuals (Almberg *et al.* 2011; Potapov *et al.* 2011). However, when applying the risk model its ability to predict new disease cases needs to be continually evaluated. Local managers can utilize the ~3000 - 5000 deer tested annually for CWD in Alberta (Pybus 2012) for model evaluation. With each additional year of CWD surveillance data the opportunity exists to refine and improve the model to ensure it continues to predict with high accuracy and precision.

Literature Cited

- Almberg, E.S., Cross, P.C., Johnson, C.J., Heisey, D.M. & Richards, B.J. (2011) Modeling routes of chronic wasting disease transmission: Environmental prion persistence promotes deer population decline and extinction. *Plos One*, **6**, e19896.
- Beest, D.E.t., Hagenars, T.J., Stegeman, J.A., Koopmans, M.P.G. & van Boven, M. (2011) Risk based culling for highly infectious diseases of livestock. *Veterinary Research*, **42**, 81.
- Bellan, S.E. (2010) The importance of age dependent mortality and the extrinsic incubation period in models of mosquito-borne disease transmission and control. *Plos One*, **5**, e10165.
- Blanchong, J.A., Samuel, M.D., Scribner, K.T., Weckworth, B.V., Langenberg, J.A. & Filcek, K.B. (2008) Landscape genetics and the spatial distribution of chronic wasting disease. *Biology Letters*, **4**, 130-133.
- Clements, G.M., Hygnstrom, S.E., Gilsdorf, J.M., Baasch, D.M., Clements, M.J. & Vercauteren, K.C. (2011) Movements of white-tailed deer in riparian habitat: Implications for infectious diseases. *Journal of Wildlife Management*, **75**, 1436-1442.
- Conner, M.M. & Miller, M.W. (2004) Movement patterns and spatial epidemiology of a prion disease in mule deer population units. *Ecological Applications*, **14**, 1870-1881.
- Conner, M.M., Gross, J.E., Cross, P.C., Ebinger, M.R., Gillies, R.R. & Miller, M.W. (2007) Scale-dependent approaches to modeling spatial epidemiology of chronic wasting disease. *Ecological Applications*, **17**, 140-153.
- Cullingham, C.I., Merrill, E.H., Pybus, M.J., Bollinger, T.K., Wilson, G.A. & Coltman, D.W. (2011) Broad and fine-scale genetic analysis of white-tailed deer populations: Estimating the relative risk of chronic wasting disease spread. *Evolutionary Applications*, **4**, 116-131.
- Diefenbach, D.R., Long, E.S., Rosenberry, C.S., Wallingford, B.D. & Smith, D.R. (2008) Modeling distribution of dispersal distances in male white-tailed deer. *Journal of Wildlife Management*, **72**, 1296-1303.
- Dobson, F. (1982) Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, **30**, 1183-1192.
- Farnsworth, M.L., Wolfe, L.L., Hobbs, N.T., Burnham, K.P., Williams, E.S., Theobald, D.M., Conner, M.M. & Miller, M.W. (2005) Human land use

- influences chronic wasting disease prevalence in mule deer. *Ecological Applications*, **15**, 119-126.
- Fretwell, S.D. & Lucas Jr, H.L. (1970) On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor*, **19**, 16-36.
- Frost, C.J., Hygnstrom, S.E., Tyre, A.J., Eskridge, K.M., Baasch, D.M., Boner, J.R., Clements, G.M., Gilsdorf, J.M., Kinsell, T.C. & Vercauteren, K.C. (2009) Probabilistic movement model with emigration simulates movements of deer in nebraska, 1990-2006. *Ecological Modelling*, **220**, 2481-2490.
- Gaillard, J., Coulson, T. & Festa-Bianchet, M. (2010) Demographic processes: Lessons from long-term, individual-based studies. *Dynamics of Large Herbivore Populations in Changing Environments : Towards Appropriate Models* Anonymous pp. 98-116. Chichester, West Sussex, UK; Hoboken, NJ, Wiley-Blackwell.
- Gaillard, J., Festa-Bianchet, M., Yoccoz, N., Loison, A. & Toigo, C. (2000) Temporal variation in fitness components and population dynamics of large herbivores RID A-1493-2008. *Annual Review of Ecology and Systematics*, **31**, 367-393.
- Garlick, M.J., Powell, J.A., Hooten, M.B. & McFarlane, L.R. (2011) Homogenization of large-scale movement models in ecology. *Bulletin of Mathematical Biology*, **73**, 2088-2108.
- Gilbert, M., Mitchell, A., Bourn, D., Mawdsley, J., Cliton-Hadley, R. & Wint, W. (2005) Cattle movements and bovine tuberculosis in great britain. *Nature*, **435**, 491-496.
- Gross, J.E. & Miller, M.W. (2001) Chronic wasting disease in mule deer: Disease dynamics and control. *Journal of Wildlife Management*, **65**, 205-215.
- Johnson, C.J., Phillips, K.E., Schramm, P.T., McKenzie, D., Aiken, J.M. & Pedersen, J.A. (2006) Prions adhere to soil minerals and remain infectious. *Plos Pathogens*, **2**, 296-302.
- Joly, D.O., Samuel, M.D., Langenberg, J.A., Blanchong, J.A., Batha, C.A., Rolley, R.E., Keane, D.P. & Ribic, C.A. (2006) Spatial epidemiology of chronic wasting disease in wisconsin white-tailed deer. *Journal of Wildlife Diseases*, **42**, 578-588.
- Langenberg, J.A., Miller, M.W. & Creekmore, L. (2008) *Alberta Chronic Wasting Disease Management Program Review Panel Report*.
<http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDi>

sease/documents/AlbertaCWDMManagement-ProgramReviewPanelReport-Feb2008.pdf

- Loe, L.E., Mysterud, A., Veiberg, V. & Langvatn, R. (2009) Negative density-dependent emigration of males in an increasing red deer population. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 2581-2587.
- Long, E.S., Diefenbach, D.R., Rosenberry, C.S. & Wallingford, B.D. (2008) Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. *Behavioral Ecology*, **19**, 1235-1242.
- Matthysen, E. (2005) Density-dependent dispersal in birds and mammals. *Ecography*, **28**, 403-416.
- McLoughlin, P.D., Boyce, M.S., Coulson, T. & Clutton-Brock, T. (2006) Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B-Biological Sciences*, **273**, 1449-1454.
- McLoughlin, P.D., Gaillard, J.-., Boyce, M.S., Bonenfant, C., Messier, F., Duncan, P., Delorme, D., Van Moorter, B., Said, S. & Klein, F. (2007) Lifetime reproductive success and composition of the home range in a large herbivore. *Ecology*, **88**, 3192-3201.
- Meyers, L., Pourbohloul, B., Newman, M., Skowronski, D. & Brunham, R. (2005) Network theory and SARS: Predicting outbreak diversity. *Journal of Theoretical Biology*, **232**, 71-81.
- Miller, M.W. & Williams, E.S. (2003) Horizontal prion transmission in mule deer. *Nature*, **425**, 35-36.
- Miller, M.W., Williams, E.S., Hobbs, N.T. & Wolfe, L.L. (2004) Environmental sources of prion transmission in mule deer. *Emerging Infectious Diseases*, **10**, 1003-1006.
- Miller, M.W., Williams, E.S., McCarty, C.W., Spraker, T.R., Kreeger, T.J., Larsen, C.T. & Thorne, E.T. (2000) Epizootiology of chronic wasting disease in free-ranging cervids in Colorado and Wyoming. *Journal of Wildlife Diseases*, **36**, 676-690.
- Miller, M.W., Hobbs, N.T. & Tavener, S.J. (2006) Dynamics of prion disease transmission in mule deer. *Ecological Applications*, **16**, 2208-2214.
- Nielsen, S.E., Stenhouse, G.B. & Boyce, M.S. (2006) A habitat-based framework for grizzly bear conservation in Alberta. *Biological Conservation*, **130**, 217-229.

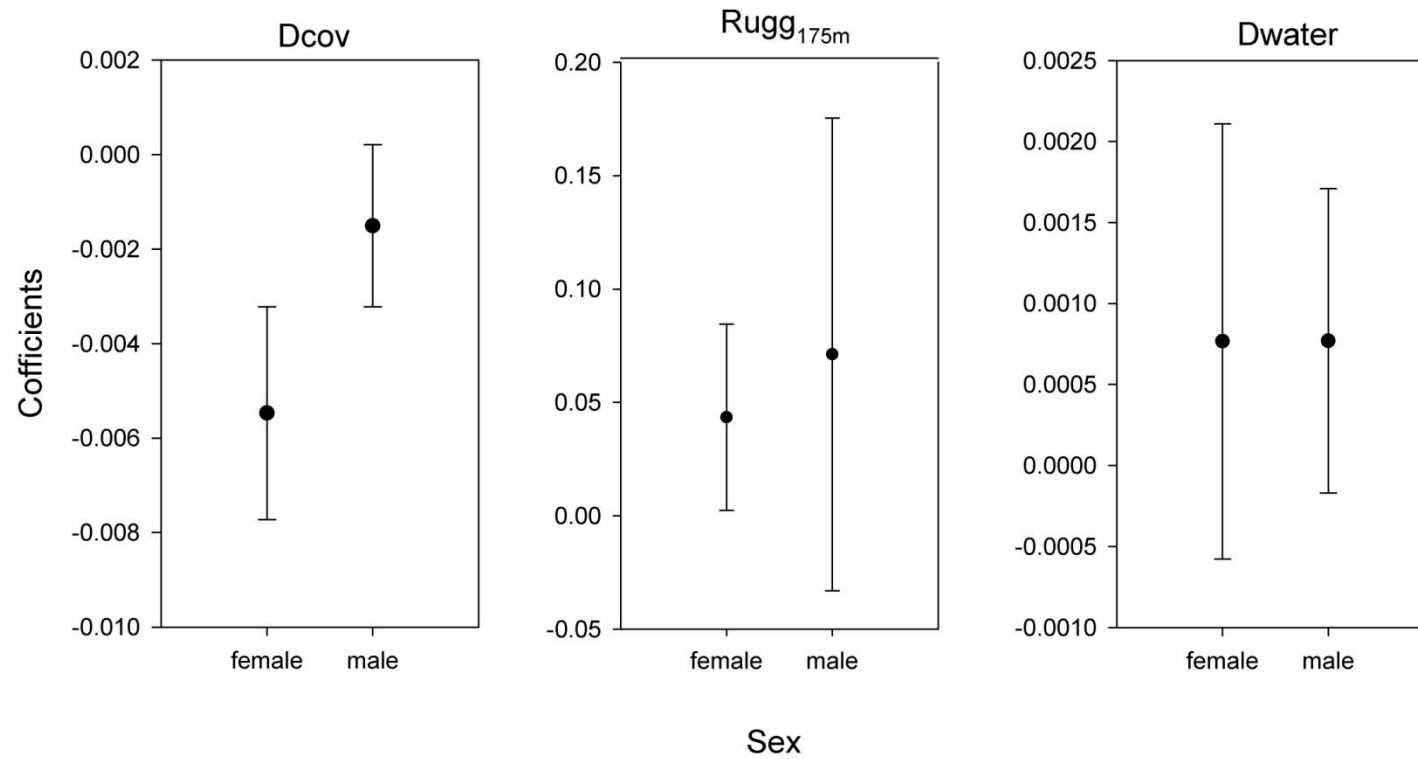
- Nixon, C.M., Hansen, L.P., Brewer, P.A., Chelsvig, J.E., Sullivan, J.B., Esker, T.L., Koerkenmeier, R., Etter, D.R., Cline, J. & Thomas, J.A. (1994) Behavior, dispersal, and survival of male white-tailed deer in illinois. *Illinois Natural History Survey Biological Notes*, **139**, 1-30.
- Osnas, E.E., Heisey, D.M., Rolley, R.E. & Samuel, M.D. (2009) Spatial and temporal patterns of chronic wasting disease: Fine-scale mapping of a wildlife epidemic in wisconsin. *Ecological Applications*, **19**, 1311-1322.
- Pongsumpun, P., Lopez, D.G., Favier, C., Torres, L., Llosa, J. & Dubois, M.A. (2008) Dynamics of dengue epidemics in urban contexts. *Tropical Medicine & International Health*, **13**, 1365-3156.
- Potapov, A., Merrill, E. & Lewis, M.A. (2012) Wildlife disease elimination and density dependence. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 3139-3145.
- Potapov, A., Merrill, E.H., Pybus, M., Coltman, D.W. & Lewis, M. (2011) Chronic wasting disease: On possible transmission mechanisms in deer. *Proceedings of the Royal Society*, **279**, 3139-3145.
- Pybus, M. (2012) CWD Program Review. *Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta*.
<http://www.srd.alberta.ca/FishWildlife/WildlifeDiseases/ChronicWastingDisease/documents/CWD-ProgramReview-May-2012.pdf>
- Rascalou, G., Pontier, D., Menu, F. & Gourbiere, S. (2012) Emergence and prevalence of human vector-borne diseases in sink vector populations. *Plos One*, **7**, e36858.
- Rees, E.E., Merrill, E.H., Bollinger, T.K., Ten Hwang, Y., Pybus, M.J. & Coltman, D.W. (2012) Targeting the detection of chronic wasting disease using the hunter harvest during early phases of an outbreak in saskatchewan, canada. *Preventive Veterinary Medicine*, **104**, 149-159.
- Remais, J., Akullian, A., Ding, L. & Seto, E. (2010) Analytical methods for quantifying environmental connectivity for the control and surveillance of infectious disease spread. *Journal of the Royal Society Interface*, **7**, 1181-1193.
- Shaw, J.C., Lancia, R.A., Conner, M.C. & Rosenberry, C.S. (2006) Effect of population demographics and social pressures on white-tailed deer dispersal ecology. *Journal of Wildlife Management*, **70**, 1293-1301.
- Tamgueney, G., Miller, M.W., Wolfe, L.L., Sirochman, T.M., Glidden, D.V., Palmer, C., Lemus, A., DeArmond, S.J. & Prusiner, S.B. (2009)

Asymptomatic deer excrete infectious prions in faeces. *Nature*, **461**, 529-U90.

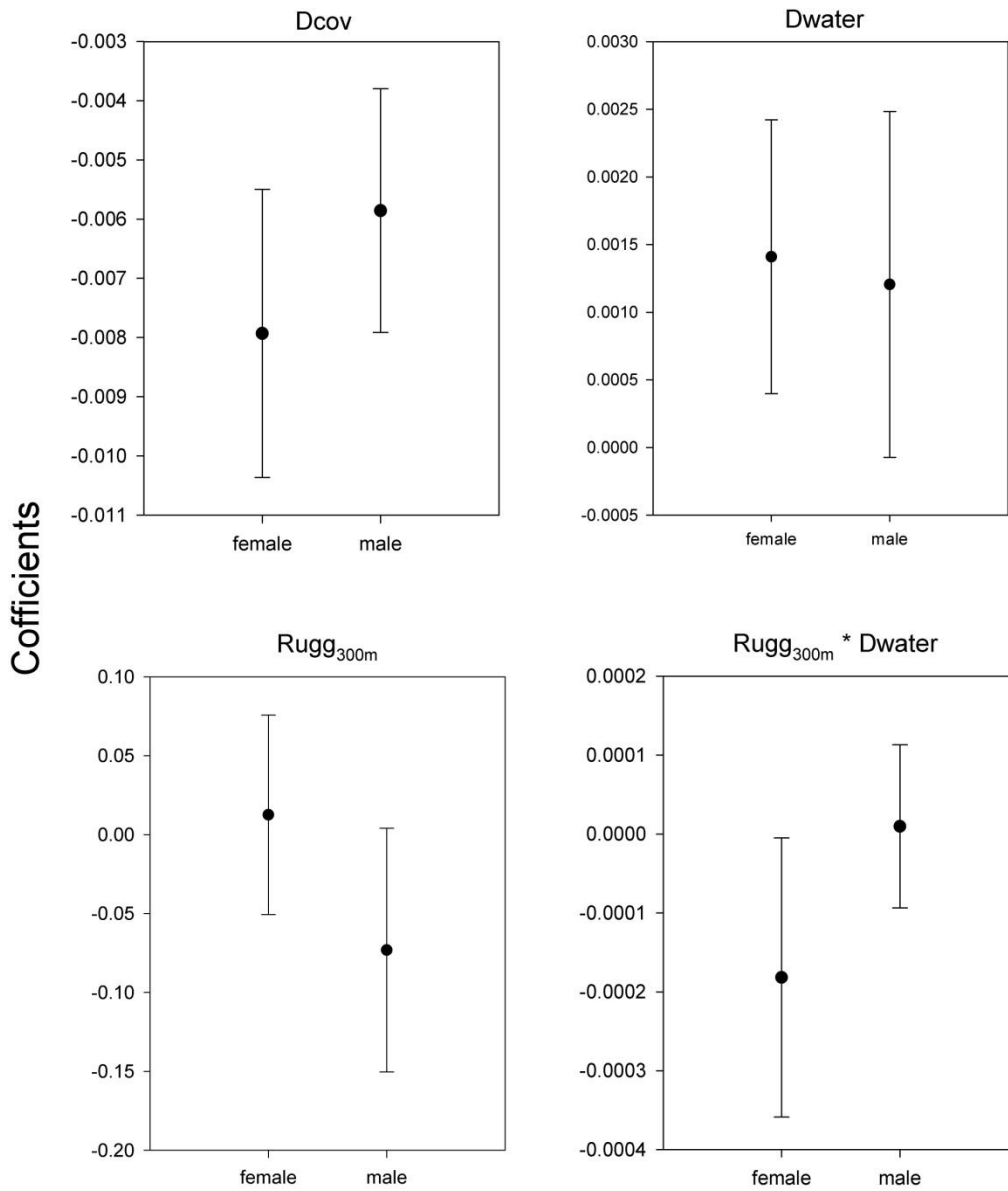
Tildesley, M.J., Bessell, P.R., Keeling, M.J. & Woolhouse, M.E.J. (2009) The role of pre-emptive culling in the control of foot-and-mouth disease. *Proceedings of the Royal Society B-Biological Sciences*, **276**, 3239-3248.

Williams, E.S. & Miller, M.W. (2003) Prions in the wild: CWD in deer and elk. *Microbiology Today*, **30**, 172-173.

APPENDICES



Appendix 1.A. Coefficients and standard errors for male ($n = 8$) and female ($n = 12$) mule deer step selection function models. Deer were deployed with GPS-collars between 2006-2008 in east-central Alberta and west-central Saskatchewan. Standard errors (SE) were adjusted using sandwich variance estimation with clustering by individual deer (Rogers 1993; Williams 2000). Corresponding covariates (Dcov, Rugg_{175m} and Dwater) are described in Table 2.1.



Sex

Appendix 1.B. Coefficients and standard errors for male (n = 5) and female (n = 13) white-tailed deer step selection function models. Deer were deployed with GPS-collars between 2006-2008 in east-central Alberta and west-central Saskatchewan. Standard errors (SE) were adjusted using sandwich variance estimation with clustering by individual deer (Rogers 1993; Williams 2000). Corresponding covariates (Dcov, Rugg_{300m} and Dwater) are described in Table 2.1.

Appendix 2.A. Estimated 2011 pre-hunting season populations of mule deer (MUDE) and white-tailed (WTDE) in 7 wildlife management units (WMU) in east-central Alberta. Estimates were based on winter aerial surveys and hunter success within the WMUs.

WMU	MUDE	WTDE	MUDE/WTDE
203	2470	1250	1.98
730	2211	1703	1.30
232	2033	2107	0.96
238	547	1533	0.36
254	1040	2342	0.44
258	700	4200	0.17
500	500	4000	0.13

Appendix 2.B.

The deer population model, used to extrapolate population across years, incorporated hunter-harvest success rates (14 to 94% success) determined via telephone and internet surveys, winter survival rates (70 to 85% survival) based on winter severity and fawn recruitment (35 to 70 fawns per 100 does, Dave Moore Personal Communications). For simplicity, I assumed constant male to female ratios of 30 males to 70 females for mule deer and 25 males to 75 females for white-tailed deer because data were limited across WMUs. These ratios were based on an average of 7 winter flight surveys across 7 of the 15 AB WMUs within the study area between 2005 and 2011.

Appendix 2.C. Sex ratios for mule and white-tailed deer during winter aerial population surveys in east-central Alberta from 2005 to 2011. The number of bucks and fawns are reported per 100 does. The calculated % males and % females includes fawns with an assumed 50/50 sex ratio.

WMU	Year	Mule deer				White-tailed deer			
		Bucks	Fawns	% Male	% Female	Bucks	Fawns	% Male	% Female
234	2005	31	61	32	68	16	58	26	74
258	2008	22	63	20	71	27	53	30	70
236	2009	16	18	19	81	19	18	20	80
256	2009	27	20	25	75	22	51	27	73
232	2010	42	75	37	63	18	53	26	74
202	2011	51	61	38	62	19	35	24	76
730	2011	31	65	32	68	13	39	21	79

Appendix 3.A. Empirical turn angle frequency distribution used to draw available steps for the step selection function analysis. Bin frequencies were averaged across 20 mule deer (male = 8; female = 12) and 18 white-tailed deer (male = 5; female = 13). Movements were obtained from 2-hour relocation data collected via GPS collars deployed between 2006-2008 in east-central Alberta and west-central Saskatchewan.

Min (°)	Max (°)	Mean Frequency	SD
-180	-156	0.07601	0.01680
-156	-132	0.06486	0.01039
-132	-108	0.05899	0.00981
-108	-84	0.05864	0.00889
-84	-60	0.06177	0.00927
-60	-36	0.06357	0.00837
-36	-12	0.07282	0.00905
-12	12	0.07235	0.01116
12	36	0.07091	0.01136
36	60	0.06812	0.00995
60	84	0.06415	0.01003
84	108	0.06278	0.01179
108	132	0.06083	0.01197
132	156	0.06603	0.01299
156	180	0.07819	0.01020

Appendix 3.B. Empirical step length frequency distribution used to draw available steps as part of the step selection function analysis. Bin frequencies were averaged across 18 white-tailed deer (WTDE, male = 5, female = 13), 8 male mule deer (MUDE Male) and 12 female mule deer (MUDE Female). Movements were obtained from 2-hour relocation data collected via GPS collars deployed between 2006-2008 in east-central Alberta and west-central Saskatchewan.

Min (m)	Max (m)	WTDE		MUDE Male		MUDE Female	
		Mean	SD	Mean	SD	Mean	SD
0	50	0.278068	0.041331	0.382295	0.075415	0.338133	0.052192
50	100	0.141840	0.026016	0.116702	0.025864	0.156958	0.019729
100	150	0.103826	0.020329	0.090281	0.015566	0.097876	0.015310
150	200	0.074209	0.017745	0.063510	0.014476	0.070176	0.011019
200	250	0.060002	0.013742	0.052204	0.011982	0.055628	0.012397
250	300	0.049996	0.010437	0.040460	0.010622	0.041163	0.008445
300	350	0.037517	0.009519	0.035696	0.011877	0.033941	0.008102
350	400	0.031931	0.005799	0.026242	0.006826	0.027237	0.004082
400	450	0.027268	0.005177	0.024475	0.005328	0.025730	0.005066
450	500	0.024126	0.006607	0.017421	0.005480	0.022816	0.007627
500	550	0.020374	0.004805	0.016391	0.004355	0.018215	0.006775
550	600	0.018620	0.005990	0.014088	0.003338	0.015348	0.004909
600	650	0.014610	0.005687	0.014737	0.006312	0.012868	0.004192
650	700	0.011913	0.004311	0.013115	0.005408	0.011087	0.003866
700	750	0.011564	0.004643	0.007799	0.004831	0.009753	0.003757
750	800	0.009799	0.003996	0.009158	0.001856	0.008617	0.003357
800	850	0.008346	0.004073	0.008157	0.003833	0.006122	0.002316
850	900	0.007929	0.004313	0.008242	0.004057	0.004680	0.003332
900	950	0.006883	0.003990	0.006176	0.003549	0.004332	0.003112
950	1000	0.006044	0.003521	0.006038	0.003915	0.004641	0.001976
1000	1050	0.004910	0.003898	0.004721	0.002967	0.002919	0.001886
1050	1100	0.005151	0.003601	0.005046	0.004533	0.003240	0.001963
1100	1150	0.003759	0.002231	0.003606	0.002725	0.003201	0.001798
1150	1200	0.004645	0.003171	0.002356	0.001772	0.003416	0.001878
1200	1250	0.003502	0.002773	0.003420	0.002161	0.001606	0.001084
1250	1300	0.003024	0.002545	0.002847	0.001840	0.001925	0.001510
1300	1350	0.002976	0.002903	0.002009	0.001864	0.001669	0.001190
1350	1400	0.002390	0.002193	0.001491	0.000877	0.002083	0.001611
1400	1450	0.002607	0.002749	0.001730	0.001525	0.001385	0.001404
1450	1500	0.002889	0.004571	0.001638	0.001257	0.001301	0.001472
1500	1550	0.002036	0.002204	0.002175	0.002367	0.001221	0.001155
1550	1600	0.001926	0.001690	0.001123	0.001471	0.000773	0.000822
1600	1650	0.001148	0.001468	0.001701	0.001191	0.000927	0.000970
1650	1700	0.001833	0.001746	0.001537	0.001894	0.000654	0.000655
1700	1750	0.001643	0.002570	0.001072	0.000752	0.000520	0.000754
1750	1800	0.001022	0.001479	0.001168	0.000814	0.000620	0.000723

Appendix 3.B. Continued

Min (m)	Max (m)	WTDE		MUDE Male		MUDE Female	
		Mean	SD	Mean	SD	Mean	SD
1800	1850	0.001588	0.002394	0.000836	0.001170	0.000895	0.001139
1850	1900	0.000787	0.000977	0.000649	0.000638	0.000668	0.000826
1900	1950	0.000614	0.000868	0.001564	0.002629	0.000530	0.000702
1950	2000	0.000693	0.000939	0.001499	0.002660	0.000830	0.000602
2000	2050	0.000671	0.000907	0.000392	0.000429	0.000669	0.000898
2050	2100	0.000988	0.001321	0.000277	0.000387	0.000549	0.000589
2100	2150	0.000523	0.000944	0.000316	0.000439	0.000332	0.000719
2150	2200	0.000472	0.000678	0.000236	0.000360	0.000257	0.000626
2200	2250	0.000526	0.000749	0.000486	0.000915	0.000429	0.000585
2250	2300	0.000554	0.000835	0.000347	0.000578	0.000206	0.000422
2300	2350	0.000352	0.000596	0.000327	0.000383	0.000206	0.000379
2350	2400	0.000165	0.000311	0.000039	0.000110	0.000413	0.000947
2400	2450	0.000337	0.000547	0.000535	0.000687	0.000183	0.000472
2450	2500	0.000211	0.000391	0.000117	0.000331	0.000336	0.000505
2500	2550	0.000130	0.000291	0.000161	0.000240	0.000221	0.000454
2550	2600	0.000165	0.000316	0.000346	0.000532	0.000179	0.000621
2600	2650	0.000097	0.000412	0.000039	0.000110	0.000000	0.000000
2650	2700	0.000172	0.000368	0.000465	0.000494	0.000053	0.000183
2700	2750	0.000193	0.000416	0.000000	0.000000	0.000118	0.000277
2750	2800	0.000119	0.000252	0.000000	0.000000	0.000026	0.000091
2800	2850	0.000036	0.000104	0.000078	0.000220	0.000000	0.000000
2850	2900	0.000057	0.000178	0.000255	0.000606	0.000065	0.000226
2900	2950	0.000118	0.000248	0.000117	0.000232	0.000000	0.000000
2950	3000	0.000111	0.000230	0.000091	0.000256	0.000053	0.000183

Appendix 4. Spearman’s rank correlation coefficients (bottom left) and associated P-values (top right) between landscape covariates in the white-tailed deer step selection function (WTDE-SSF) and mule deer SSF (MUDE-SSF). Correlation was calculated using 3,564 observed steps for 18 white-tailed deer and 2,320 steps from 20 mule deer. Covariate descriptions are provided in Table 2.1.

WTDE-SSF	Dcov	Dwater	Rugg _{300m}
Dcov		<0.01	0.33
Dwater	-0.09		<0.01
Rugg _{300m}	-0.02	-0.34	

MUDE-SSF	Dcov	Dwater	Rugg _{175m}
Dcov		0.58	<0.01
Dwater	0.01		<0.01
Rugg _{175m}	-0.06	-0.38	

Appendix 5. Competing P_{IDM} base models ranked by Akaike’s information criterion (AIC) of the probability that a harvested deer is CWD+ based on only deer characteristics and with no landscape covariates. Models were derived using 4957 mule and white-tailed deer (94 CWD+; 4863 CWD-) harvested between 2005 and 2010 in eastern-Alberta and western-Saskatchewan. Included are the number of estimated parameters (k) and AIC weight (w_i) for each model. Covariate descriptions in Table 2.1.

P_{IDM}	Covariates	k	AIC	ΔAIC	w_i
1	Province, Harvest, Time, Species, Sex	7	839.7	0.0	0.99
2	1 – Sex	6	849.7	10.0	<0.01
3	1 - Harvest	6	850.8	11.1	<0.01
4	1 - Time	6	852.3	12.5	<0.01
5	1 - Species	6	870.1	30.4	<0.01
6	1 - Province	6	893.5	53.7	<0.01

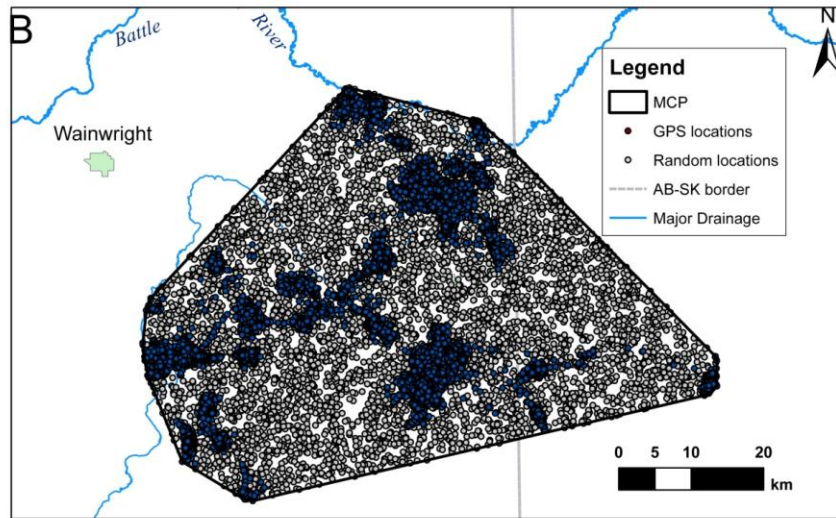
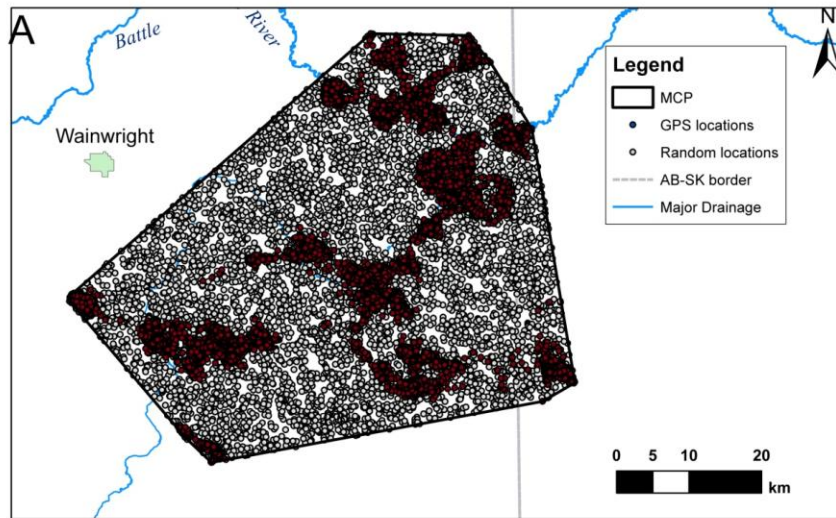
Appendix 6. Descriptive metrics for five landscape covariates calculated for 4957 mule and white-tailed deer used to create the P_{IDM} CWD risk model. The covariates include distance to road (Droad), terrain ruggedness (Rugg_{12km}), stream density (Stream_{3km}), proportion of agriculture (Agri_{12km}) and landscape connectivity measured as resistance ($M_{Resistance}$). Detailed covariate descriptions in Table 2.1.

Metric	Droad	Rugg _{12km}	Stream _{3km}	Agri _{12km}	$M_{Resistance}$
Mean	627.86	11.76	1313.02	0.53	182.28
Minimum	0.00	0.98	0.00	0.00	0.57
1st quartile	223.61	6.62	0.00	0.26	1.05
Median	509.90	9.36	0.00	0.56	1.32
3rd quartile	800.00	14.22	2258.11	0.82	1.82
Maximum	4669.05	52.68	12301.22	1.00	466800.68

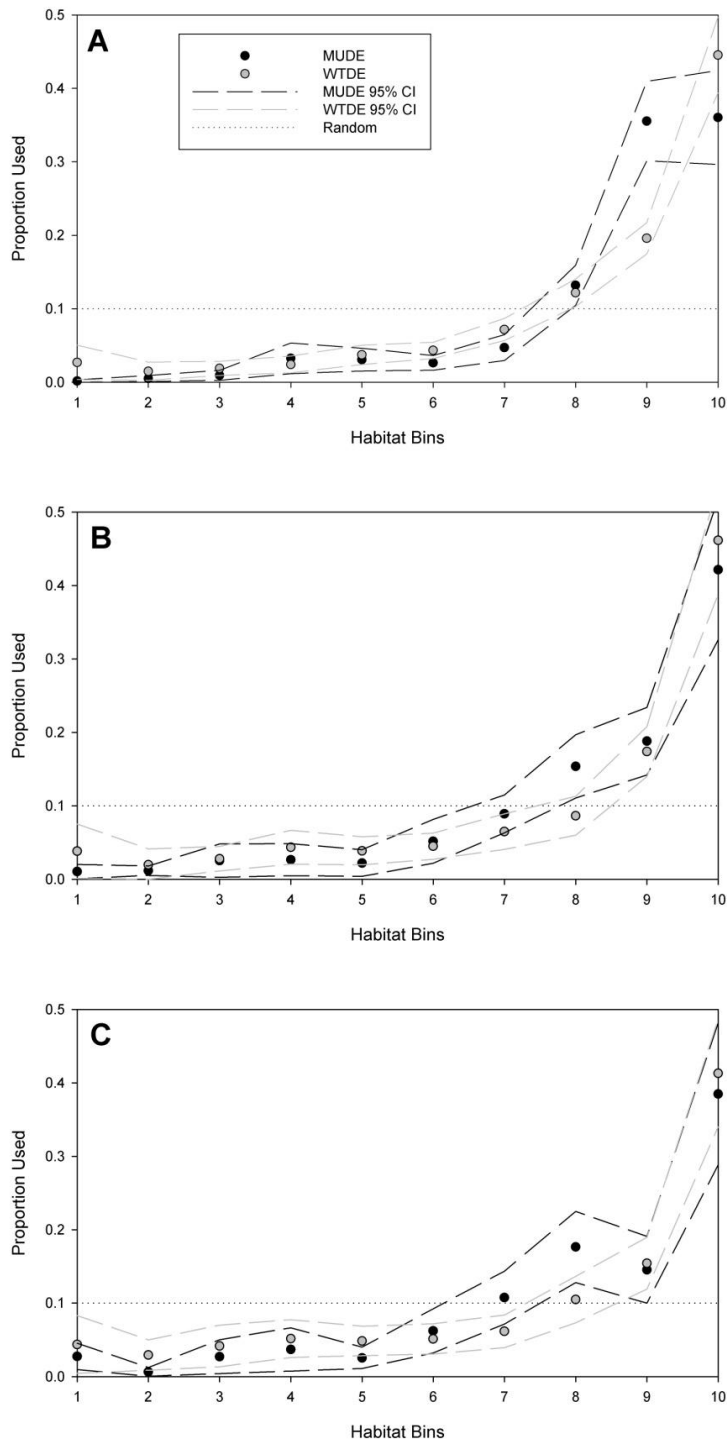
Appendix 7. GPS collars were tested for location accuracy and fix rate success prior to deployment on captured deer. Collars were hung in a stationary position at a height of 1 m for a period of 1 to 7 days. Nine collars were tested in eight different locations in deciduous forest, shrubs or open grassland habitat. Of 1148 fix attempts during the trial 1142 were successful, equating to a 99.4% fix success rate. The average location error for successful fixes was 7.5 ± 8.4 m (SD).

Appendix 8. Details of the GPS location data used to calculate the RSPF for each season (summer, winter and hunting). Including the number of deer collared (No.deer) and the total, mean, standard deviation (SD), median, minimum and maximum number of locations across all deer.

Metrics	Mule deer				White-tailed deer			
	All Year	Summer	Winter	Hunting	All Year	Summer	Winter	Hunting
No.deer	22	22	22	22	24	24	24	24
Total	76463	45161	31302	22865	78515	46497	32018	23296
Mean	3476	2053	1423	1039	3271	1937	1334	971
SD	845	553	343	290	951	609	378	303
Median	3074	1908	1354	869	3046	1831	1341	865
Minimum	2072	1217	855	637	1848	1084	752	525
Maximum	5102	2903	2216	1484	5057	2878	2207	1477



Appendix 9. The available locations, used to create resource selection probability functions, for mule deer (A) and white-tailed deer (B) drawn randomly from within a minimum convex polygon (MCP) encompassing their used locations recorded with GPS collars.



Appendix 10. Proportion of locations from an independent set of VHF and GPS-collared female deer ($n = 186$) within ten ranked quantile bins of seasonal RSPF values for A) the whole year, B) summer and C) the hunting season. The dotted-line represents the expected proportion of locations (0.10) if selection is random. These results were used to classify unattractive, secondary habitat and primary habitat.

Appendix 11. Mean and standard deviation (SD) of habitat covariates used to standardize the covariates in the RSPF analysis. These standardizing metrics were calculated based on locations of GPS collared female mule (n = 22) and white-tailed deer (n = 24) collected throughout the year for a total of 18700 and 20400 locations among mule and white-tailed deer respectively.

Species	Covariate	Mean	SD
White-tailed deer	Cover _{120m}	0.50	0.38
	Edge _{1km}	4.95	1.80
	Agri _{5km}	0.47	0.20
	Rugg _{500m}	5.75	5.22
	Stream _{1km}	0.45	0.73
	Road _{1km}	0.69	0.65
Mule deer	Cover _{1km}	0.40	0.23
	Grass _{500m}	0.18	0.18
	Rugged _{500m}	7.28	6.85
	Stream _{1km}	0.73	1.01
	Road _{500m}	0.71	0.88
	Well _{1km}	1.58	3.27

Appendix 12. The mean and standard deviation (SD) of vegetation biomass (g/m^2) within land cover types in east-central Alberta. Vegetation biomass was measured using clip plots corrected for the amount of visually estimated senescent vegetation in multiple 25-m and 50-m transects (n).

Cover Type	Forbs		Grasses		Shrubs		Total		n
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
Cropland	86.2	81.1	94.7	91.5	2.6	9.9	183.5	108.4	15
Forest	9.4	7.7	55.3	46.9	27.5	27.7	92.2	51.3	23
Shrubland	15.6	12.8	44.4	32.4	53.8	84.0	113.8	86.1	52
Grassland	19.2	17.6	42.3	29.3	0.4	25.9	61.9	50.8	35
Wetland	20.7	39.1	117.7	105.3	54.7	101.8	193.0	129.9	44

Appendix 13. Coefficients for models relating basal diameter to biomass of twig current annual growth and leaves for various species of shrubs that occur in the Border Deer Study area. Models were either power (P) or linear (L) functions of the form $y = ax^b$ or $y = ax - b$, respectively, where y is biomass (g) and x is basal diameter (mm).

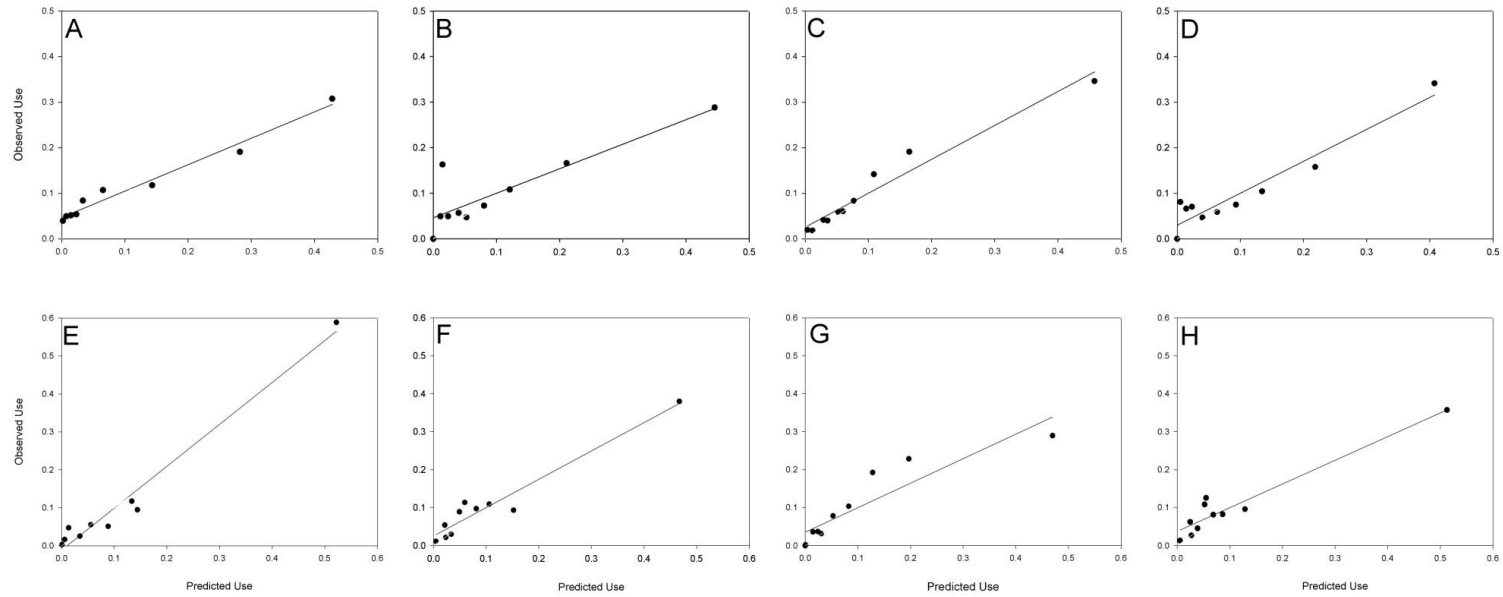
Species	Leaves					Twig CAG				
	model	a	b	n	r ²	model	a	b	n	r ²
<i>Rosa</i> spp.	P	0.1428	1.5637	30	0.35	P	0.0251	2.1116	30	0.51
<i>Elaeagnus</i> spp.	L	0.8319	4.4846	12	0.63	L	0.7272	4.0386	12	0.72
<i>Prunus</i> spp.	P	0.2255	1.3107	29	0.19	P	0.0616	1.5809	29	0.19
<i>Ribes</i> spp.	P	0.0008	3.4979	6	0.80	L	0.1189	0.2583	6	0.09
<i>Symphoricarpos albus</i>	P	0.0883	1.8017	14	0.37	P	0.0080	2.6000	14	0.40
<i>Amelanchier alnifolia</i>	L	0.5702	1.3659	30	0.44	P	0.6827	0.5672	30	0.07
<i>Salix</i> spp.	P	0.0504	2.0397	30	0.71	P	0.0020	2.8740	30	0.66
<i>Populus tremuloides</i>	P	0.0775	1.6836	29	0.59	P	0.0014	2.8546	29	0.77
<i>Rubus</i> spp.	P	0.4987	1.1490	7	0.75	L	0.1313	0.2898	7	0.58
<i>Cornus</i> spp.	P	0.0015	3.5359	8	0.83	P	0.0001	4.2869	8	0.75
<i>Crataegus</i> spp.	P	0.0103	2.9773	5	0.35	L	2.0583	9.8935	5	0.40
<i>Acer negundo</i>	-	-	-	-	-	-	-	-	-	-
<i>Spirea</i>	-	-	-	-	-	-	-	-	-	-
Unknown	-	-	-	-	-	-	-	-	-	-

Appendix 14. The null and the top ranked RSPF models for mule and white-tailed deer in east-central Alberta based on GPS collar locations collected throughout the year. Presented are number of model parameters (k), Bayesian information criterion difference (ΔBIC), and BIC weight (w_i). Covariate descriptions are provided in Table 3.1.

Species	Covariates	k	ΔBIC	w_i
Mule Deer	Cover _{1km} , Grass _{500m} , Rugg _{500m} , Pond, Stream _{1km} , Road _{500m} , Well _{1km}	9	0	0.99
	Cover _{1km} , Grass _{500m} , Rugg _{500m} , Pond, Stream _{240m} , Road _{500m} , Well _{1km}	9	229	<0.01
	Cover _{1km} , Grass _{1km} , Rugg _{500m} , Pond, Stream _{1km} , Road _{500m} , Well _{1km}	9	383	<0.01
	Cover _{1km} , Grass _{500m} , Rugg _{500m} , Pond, Stream _{500m} , Road _{500m} , Well _{1km}	9	426	<0.01
White-tailed Deer	Cover _{120m} , Edge _{1km} , Agri _{5km} , Agri _{5km} ² , Rugg _{500m} , Pond, Stream _{1km} , Road _{1km} , Rugg _{500m} x River	11	0	0.99
	Cover _{120m} , Edge _{1km} , Agri _{5km} , Agri _{5km} ² , Rugg _{500m} , Pond, Stream _{240m} , Road _{1km} , Rugg _{500m} x River	11	95	<0.01
	Cover _{120m} , Edge _{120m} , Agri _{5km} , Agri _{5km} ² , Rugg _{500m} , Pond, Stream _{120m} , Road _{1km} , Rugg _{500m} x River	11	109	<0.01
	Cover _{120m} , Edge _{1km} , Agri _{5km} , Agri _{5km} ² , Rugg _{500m} , Pond, Stream _{1km} , Road _{1km} , Rugg _{500m} x River	11	123	<0.01

Appendix 15. Coefficients (β) of the RSPFs for mule deer (MUDE) and white-tailed deer (WTDE) in winter and their respective standard errors (SE). Covariate descriptions provided in Table 3.1.

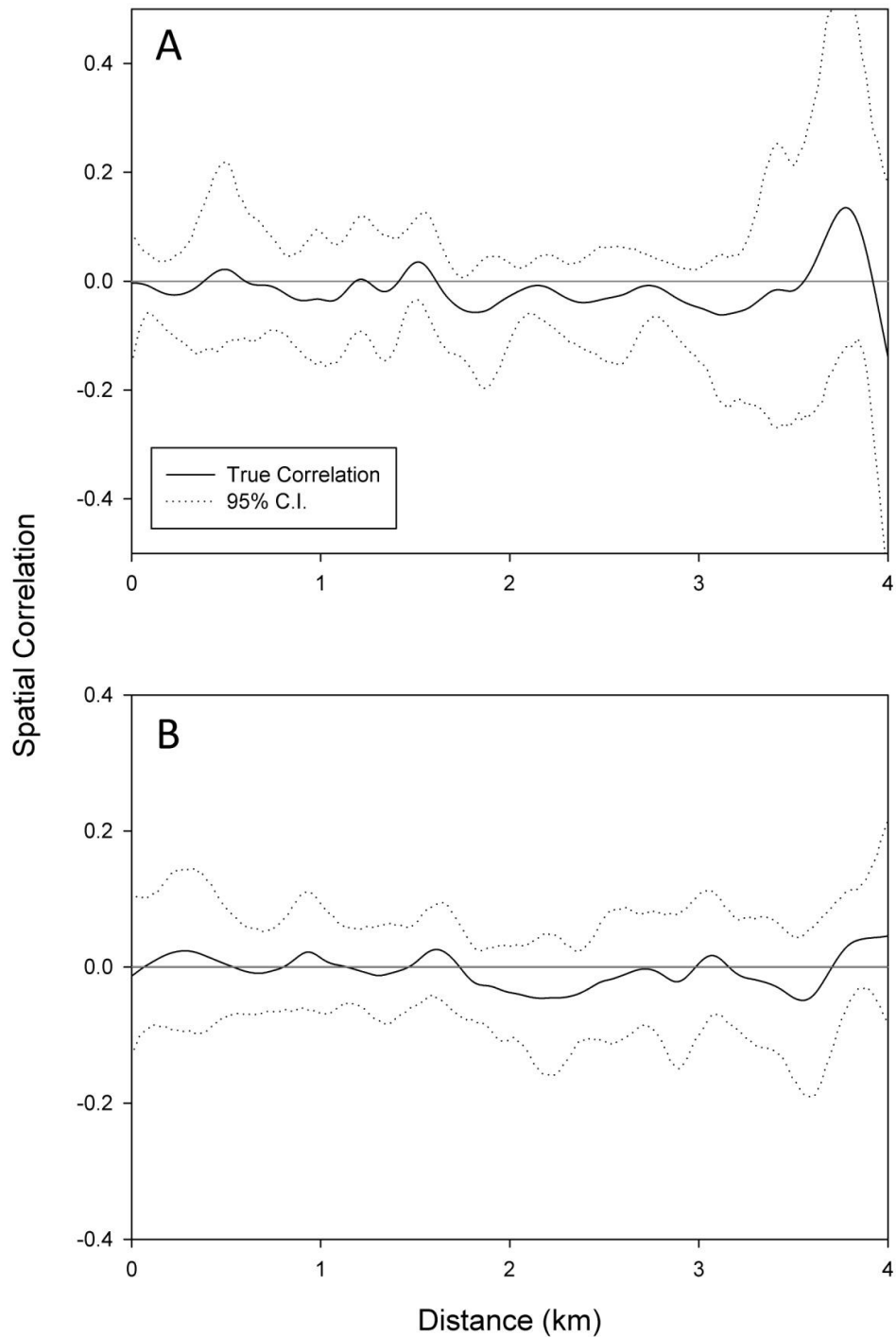
Species	Covariates	β	SE
MUDE	Intercept	-1.87	0.04
	Cover _{1km}	1.05	0.01
	Grass _{500m}	0.62	0.01
	Rugged _{500m}	0.90	0.02
	Water	-1.62	0.21
	Stream _{1km}	0.52	0.02
	Road _{500m}	-0.29	0.01
	Well _{1km}	0.03	0.01
WTDE	Intercept	-4.67	3.04
	Cover _{120m}	0.70	0.05
	Edge _{1km}	0.33	0.03
	Agri _{5km}	11.84	1.09
	Agri _{5km} ²	-11.38	1.18
	Rugged _{500m}	-0.29	0.03
	Stream _{1km}	0.10	0.04
	Water	-1.72	0.13
	Road _{1km}	-0.30	0.03
	Rugged _{500m} * River	0.53	0.08



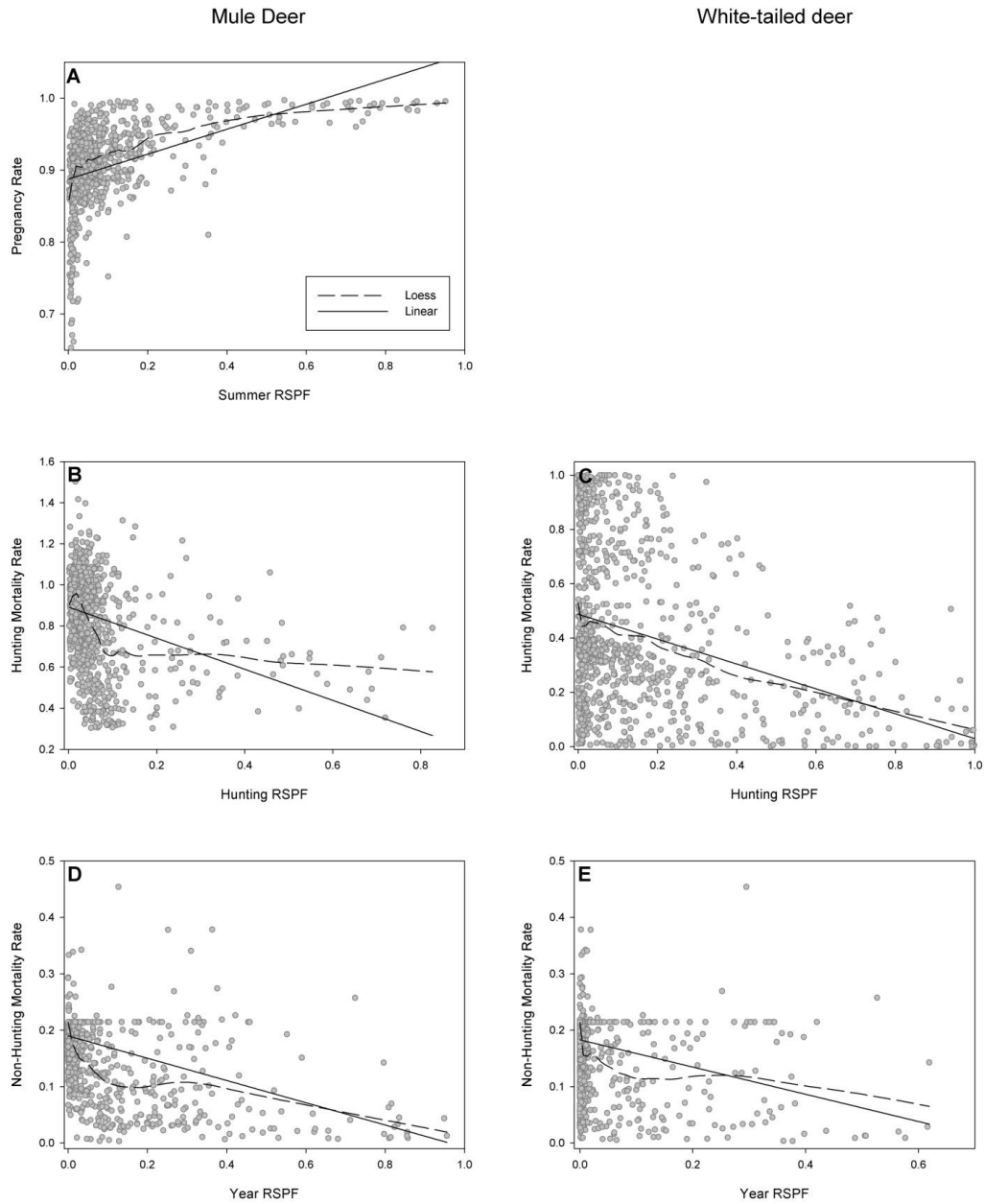
Appendix 16. Linear models fitted between the predicted values of habitat use based on seasonal RSPFs and observed use based on an independent data set of VHF and GPS collared female deer for white-tailed deer (A-D) and mule deer (E-H) during the whole year (A, E), summer (B, F), winter (C, G) and hunting season (D,H)

Appendix 17. Number of fetuses per mule and white-tailed deer harvested during the CWD herd reduction program in 2005 in wildlife management unit 234 in east-central Alberta.

No. foetus	White-tailed deer				Mule deer			
	Adult		Fawn		Adult		Fawn	
	Count	%	Count	%	Count	%	Count	%
1	34	16.0	12	70.6	3	13.6	0	0.0
2	157	73.7	5	29.4	19	86.4	0	0.0
3	20	9.4	0	0.0	0	0.0	0	0.0
4	1	0.5	0	0.0	0	0.0	0	0.0
5	1	0.5	0	0.0	0	0.0	0	0.0
Total	213	100.0	17	100.0	22	100.0	0	0.0



Appendix 18. Spline fitted to a correlogram and associated 95% confidence intervals (C.I.) measuring the degree of spatial autocorrelation in residuals of mule deer (A) and white-tailed deer (B) pregnancy models.



Appendix 19. Relationship between seasonal RSPF values (summer, hunting season and all year) and predicted values of fitness for pregnancy and mortality risk from hunting and non-hunting based on values for 1000 random locations across the study area in east-central Alberta for to either mule or white-tailed deer. A linear and loess-smoothed line are fitted to the plotted values to help visualize any trends.

Appendix 20. Winter mule deer and white-tailed deer density metrics (mean, standard deviation and median) calculated at three cell sizes based on aerial population survey from 2007 – 2009. Also reported are the *P*-values (*P*) for non-parametric Mann-Whitney U test assessing whether densities are higher in for one species.

Cell Size	Species	n	Mean	SD	Median	Mann-Whitney
25.3 km ²	White-tailed deer	187	1.41	2.07	0.46	<i>P</i> = 0.094
	Mule deer	187	1.16	1.92	0.23	
50.6 km ²	White-tailed deer	103	1.35	1.63	0.71	<i>P</i> = 0.326
	Mule deer	103	1.25	1.75	0.54	
101.2 km ²	White-tailed deer	53	1.42	1.52	1.07	<i>P</i> = 0.170
	Mule deer	53	1.15	1.60	0.42	

Appendix 21. Top ranked Poisson model of deer density at a 50.6 km² and 101.2 km² scale as a function of proportion of primary and secondary source habitat for increasing the likelihood of pregnancy, reducing the risk of hunting and non-hunting mortality, or the mean winter RSPF for mule deer (MUDE) and white-tailed deer (WTDE). All models, including the null model, possess covariates for the number of deer harvested during the herd reduction program and a random effect of grid cell over time. Presented are number of model parameters (k), Akaike's information criterion corrected for small sample size (AIC_c), AIC_c difference (ΔAIC_c), AIC_c weight (w_i).

Species	Cell Size	Covariates	k	AIC_c	ΔAIC_c	w_i
MUDE	50.6 km ²	Hunting source	4	247.3	0.0	0.92
		Non-hunting source	4	252.2	4.9	0.08
		$RSPF_{winter}$	4	259.7	12.4	<0.01
		Pregnancy source	4	273.2	25.9	<0.01
		Null model	3	276.0	28.7	<0.01
	101.2 km ²	Hunting source	4	114.6	0.0	0.75
		Non-hunting source	4	117.2	2.5	0.21
		$RSPF_{winter}$	4	120.8	6.2	0.04
		Null model	3	129.7	15.1	<0.01
		Pregnancy source	4	130.5	15.9	<0.01
WTDE	50.6 km ²	Non-hunting source	4	229.8	0.0	0.99
		$RSPF_{winter}$	4	256.4	26.6	<0.01
		Hunting source	4	257.5	27.7	<0.01
		Null model	3	276.7	46.9	<0.01
		Non-hunting source	4	110.6	0.0	0.99
	101.2 km ²	$RSPF_{winter}$	4	121.7	11.1	<0.01
		Hunting source	4	124.8	14.2	<0.01
		Null model	3	133.6	23.0	<0.01

Appendix 22. Coefficients (β) of the Poisson models for mule deer (MUDE) and white-tailed deer (WTDE) for deer densities at different scales (25.3, 50.6 and 101.2 km²) and their respective standard errors (SE) and *P*-values (*P*). Covariate Number culled is per 1000 deer.

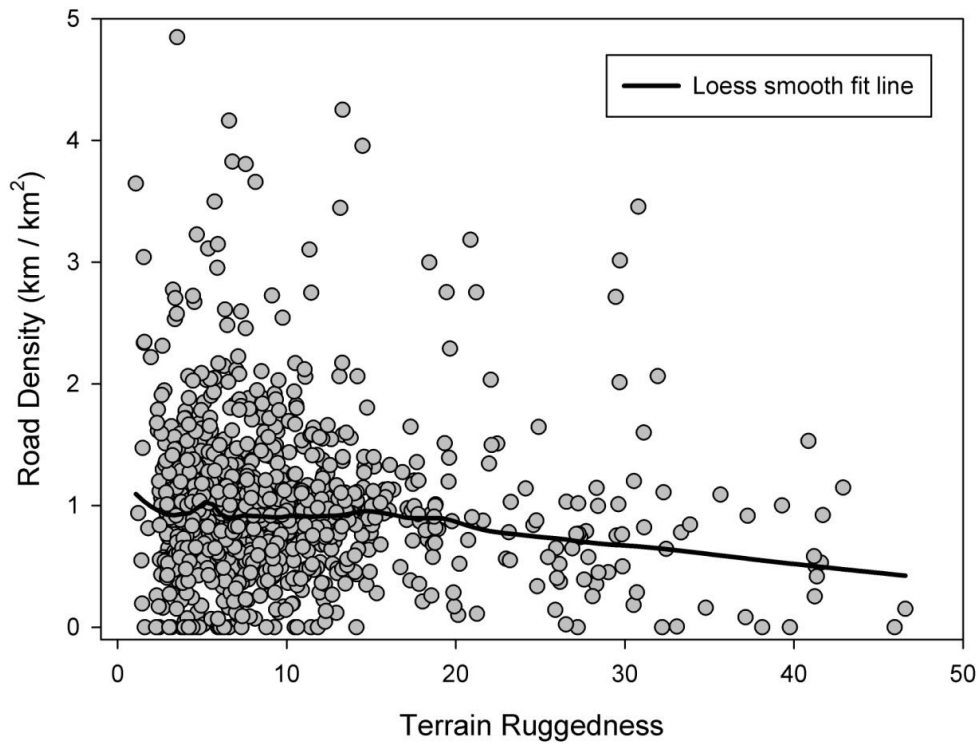
Species	Covariates	25.3 km ²			50.6 km ²			101.2 km ²		
		<i>B</i>	SE	<i>P</i>	<i>B</i>	SE	<i>P</i>	<i>B</i>	SE	<i>P</i>
Mule deer	Intercept	-1.64	0.21	<0.01	-0.96	0.22	<0.01	-1.28	0.34	<0.01
	Hunting source	2.94	0.38	<0.01	2.45	0.43	<0.01	2.93	0.66	<0.01
	Number culled	-14.53	5.43	<0.01	-10.68	4.48	0.02	-5.29	3.64	0.15
White-tailed deer	Intercept	-1.22	0.17	<0.01	-1.12	0.22	<0.01	-0.79	0.25	<0.01
	Non-hunting source	3.55	0.43	<0.01	4.06	0.58	<0.01	3.59	0.70	<0.01
	Number culled	-0.05	1.22	0.97	-0.26	1.00	0.80	-0.37	0.83	0.65

Appendix 23. Top ranked multiple and single covariate Poisson models of deer density at a 25.3 km², 50.6 km² and 101.2 km² scale as a function of proportion of primary and secondary source habitat for increasing the likelihood of pregnancy, reducing the risk of hunting and non-hunting mortality, or the mean winter RSPF for mule deer (MUDE) and white-tailed deer (WTDE). All models, including the null model, possess covariates for the number of deer harvested during the herd reduction program and a random effect of grid cell over time. Presented are number of model parameters (k), Akaike's information criterion corrected for small sample size (AIC_c), AIC difference (ΔAIC_c), AIC_c weight (w_i).

Species	Cell Size	Covariates	k	ΔAIC_c	w_i
MUDE	25.3 km ²	Hunting source	4	0.0	0.60
		Hunting source, Pregnancy source	5	1.3	0.31
		Non-hunting source	4	4.8	0.06
		Non-hunting source, Pregnancy source	5	6.8	0.02
		$RSPF_{winter}$	4	20.0	<0.01
		Pregnancy source	4	54.2	<0.01
		Null Model	3	55.8	<0.01
	50.6 km ²	Hunting source	4	0.0	0.65
		Hunting source, Pregnancy source	5	1.9	0.25
		Non-hunting source	4	4.9	0.06
		Non-hunting source, Pregnancy source	5	5.7	0.03
		$RSPF_{winter}$	4	12.5	<0.01
		Pregnancy source	4	25.9	<0.01
		Null Model	3	28.8	<0.01
	101.2 km ²	Hunting source	4	0.0	0.57
		Hunting source, Pregnancy source	5	2.2	0.19
		Non-hunting source	4	2.5	0.16
		Non-hunting source, Pregnancy source	5	4.8	0.05
		$RSPF_{winter}$	4	6.1	0.02
		Null Model	3	15.1	<0.01
		Pregnancy source	4	15.9	<0.01
WTDE	25.3 km ²	Non-hunting source	4	0.0	0.55
		Non-hunting source, Hunting source	5	0.4	0.44
		$RSPF_{winter}$	4	30.1	<0.01
		Hunting source	4	40.2	<0.01
		Null Model	3	65.9	<0.01

Appendix 23. Continued

Species	Cell Size	Covariates	k	ΔAIC_c	w_i
WTDE	50.6 km ²	Non-hunting source	4	0.0	0.64
		Non-hunting source, Hunting source	5	1.1	0.35
		$RSPF_{winter}$	4	26.6	<0.01
		Hunting source	4	27.7	<0.01
		Null Model	3	46.9	<0.01



Appendix 24. Relating road density to terrain ruggedness (standard deviation in elevation) for 1000 random locations within the study area. Both variables are calculated within a circular buffer equivalent in size to a mean female home range size (1200 m radius) for both mule and white-tailed deer.