POPULATION IMPACTS AND DISEASE PATTERNS OF HEMORRHAGIC DISEASE IN WHITE-TAILED DEER: UNDERSTANDING THE ROLE OF AN EMERGENT DISEASE

By

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ABSTRACT

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The hemorrhagic diseases (HD) epizootic hemorrhagic disease (EHD) and bluetongue (BTV) are the most significant source of viral-related mortality of deer in the United States. The emergence of HD on the landscape is affecting the population ecology of white-tailed deer (*Odocoileus virginianus*) in previously unaffected regions of North America. The forces driving apparent increases in HD are poorly understood, particularly where the disease has recently been most severe in northern latitudes. Specifically, Michigan has seen an increase in EHD related deer mortality since 2006, and 2012 was the largest outbreak of EHD in Michigan history. My research seeks to address current uncertainties for deer populations with regard to impacts from emergent HD. In this dissertation I attempt to investigate the local distribution and population-level impacts on deer in areas affected by EHD, develop and apply population estimation techniques appropriate for localized population change assessment, and evaluate landscape-level drivers of HD across an epidemiological gradient.

I estimated the annual population abundance of deer immediately after a recent EHD outbreak over a 4-year period and quantified the fine-scale spatial extent of EHD impacts associated with riparian habitats. I assessed these differences in deer abundance for sites affected and unaffected by EHD in Michigan. I determined if populations increased over time in response to local population impacts from EHD. I then validated estimates using an independent aerial survey and a novel application of N-mixture models. I evaluated the N-mixture model against distance sampling methods and tested the sensitivity of N-mixture model estimates to variation in spatial unit size. At a regional scale, I evaluated the role of drought severity in both space and time on changes in HD reports to determine if drought severity explains changing patterns of HD presence.

Important findings from my research include 1) abundance estimates in the affected area were significantly lower along transects near the river, reflecting EHD mortality associated with wetlands; 2) the opposite was true in the unaffected site; 3) estimates from both distance sampling and N-mixture modeling approaches were similar and aerial surveys using N-mixture binomial models are a practical tool for estimating abundance of a free-ranging wildlife population; 4) the selected spatial unit size in the N-mixture model had a significant effect on abundance and detection probability estimates, and their associated variance; 5) drought severity was a significant predictor of HD presence and the significance of this relationship was dependent on latitude; 6) the effect of drought was reduced or non-existent in most southern states, where the disease is endemic.

My findings suggest that EHD outbreaks will have population impacts near riparian corridors and those populations can increase post-outbreak. Further, N-mixture models may provide an improved approach to estimate populations from aerial surveys in the future, although managers and researchers should evaluate the spatial unit used for these models prior to survey implementation. While drought severity does increase the probability that HD will be detected and reported at a county level, my research points to the underlying role of acquired herd immunity across the endemic-to-emergent disease gradient

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INTRODUCTION

The emergence of an epidemic disease on the landscape is affecting the population ecology of white-tailed deer (Odocoileus virginianus) in previously unaffected regions of North America. The hemorrhagic diseases epizootic hemorrhagic disease (EHD) and bluetongue (BTV; a clinically indistinguishable hemorrhagic disease) are the most significant source of viral-related mortality of deer in the United States (Shope et al. 1960, Thomas et al. 1974). Once the virus has been transmitted to a naïve deer and onset of disease signs are observed, hemorrhaging typically leads to shock, unconsciousness, and death within 8 to 36 hours (Shope et al. 1960). Beginning in the late 1990s, the probability of EHD occurrence began to increase significantly for deer in the Northeast and Midwest regions of the United States (Stallknecht et al. 2015). In these regions, population immunity has been historically low and disease outbreaks resulting in mortality are often severe, potentially causing impacts on population abundance (Fischer et al. 1995, Gaydos et al. 2004, Howerth et al. 2001, Park et al. 2013). In epidemic regions, outbreak intensity and frequency have continued to increase significantly in the last decade (Stallknecht et al. 2015). This growing disease risk for deer populations is largely understudied and causing concern for wildlife managers and the public. My research seeks to address current uncertainties for deer populations with regard to impacts from emergent EHD.

Understanding the impact of epidemic and emerging infectious disease on wildlife populations is crucial for conservation and management as disease outbreaks intensify and spread spatially (Harvell et al. 2002, Ostfeld et al. 2005). Where EHD is epizootic, uncertainty exists regarding the complex and scale-dependent factors driving the spatial distribution of EHD. The localized spatial variation in deer mortality may be due to multiple factors including the

pathogenicity of the specific virus serotype associated with the outbreak, the ecology and competence of the disease vector, and acquired or innate host immunity dynamics (Howerth et al. 2001, Stallknecht et al. 2002, Gaydos et al. 2002a, Gaydos et al. 2002b, Gaydos et al. 2004, Ruder et al. 2015). For example, the population ecology and distribution of the vector, various midge species in the genus *Culicoides*, play a significant role in the epidemiology of hemorrhagic diseases (Mellor et al. 2000, Wilson and Mellor 2008, Savini et al. 2011). The development of larval *Culicoides* is restricted to wetland habitats and moist soils associated with river or stream banks (Wilkening et al. 1985). Further, most descriptions of detected EHD-related deer mortalities are associated with water bodies (Gaydos et al. 2004). Despite the logical connection between an increased risk of EHD for deer and wetland habitats harboring vector populations, previous research has not quantified the fine-scale spatial extent of EHD impacts associated with riparian habitats.

Climatic, environmental, and land-cover factors further affect spatial processes of EHD disease risk at regional scales and likely interact with the factors listed above (Xu et al. 2012, Berry et al. 2013, Ruder et al. 2015). In a recent review of research gaps in the epidemiology of hemorrhagic disease in North America, Ruder et al. (2015) discuss the increasing incidence and poorly understood patterns of hemorrhagic disease in northern latitudes and called for research addressing the ecology of EHD in changing environments and climates. Further, recent work by Stallknecht and colleagues (2015) stated that the significance of increases in reported hemorrhagic disease on deer population health is unknown but potential population impacts are possible. Trends in increasing disease reports across large epidemic regions of the United States warrant investigation of landscape-level factors that could be driving these patterns. Because

vector populations are sensitive to climate conditions in particular (Purse et al. 2005), changing climate patterns related to soil moisture availability and temperature should be investigated.

When sudden and severe EHD mortality events in ungulate populations occur, deer managers face considerable uncertainty in knowing the impact of EHD on the local deer population. Predicting and collecting pre-epizootic data at a scale relevant to the population impact of the disease is not possible, so assessments of direct population impacts on free-ranging deer are rare. Previous research has attempted to assess population impacts from EHD by conducting seroprevalence surveys (a measure of the level of pathogen in a population) to measure the post-outbreak immune response of a deer population or by counting deer carcasses suspected to have succumb to EHD and comparing these values to estimated background deer population estimates (Fischer et al. 1995, Gaydos et al. 2004). While past studies have provided some of the only values for free-ranging deer impacts, the background populations used were often gross calculations from regional harvest-based estimates (Fischer et al. 1995, Gaydos et al. 2004). The ability to assess disease prevalence, mortality, and predicted recovery of deer populations at appropriate scales for disease, rather than at management-unit scales, presents a clear need for the application and development of local-scale population estimation for disease studies.

Michigan is a particularly good example of a Midwestern state facing emerging and severe EHD impacts on white-tailed deer populations. Michigan has been host to one of the largest recent outbreaks at the northern range of EHD while also having one of the longest histories with the disease at northern latitudes. In 1955, researchers first confirmed epizootic hemorrhagic disease in Michigan during an outbreak event that was mirrored in New Jersey the same year (Fay et al. 1956, Shope et al. 1960). Until 2006, only one outbreak occurred after this

initial discovery, with approximately 100 dead deer reported as EHD mortalities in 1974 (MDNR). However, since 2006, Michigan had an increase in frequency and severity of EHD-related outbreaks, with EHD reports confirmed in 2006, 2008, 2009, 2010, 2011, 2012, 2013 and 2016 (MDNR). In the summer of 2012, the most severe EHD outbreak occurred in Michigan, killing at least 15,000 deer based on voluntary disease reporting and agency confirmation alone (MDNR). In that year, EHD was confirmed in 30 Michigan counties and mortalities were reported in 21 other counties during this outbreak. Deer were assumed largely naïve and the effect of EHD mortality on the deer population was a significant concern for the Michigan Department of Natural Resources and the public, as deer are a highly valued resource in the state.

The overarching goals of my research are to investigate the local distribution and population-level impacts on deer in areas affected by EHD, develop and apply population estimation techniques appropriate for localized population change assessment, and evaluate regional-level drivers of hemorrhagic disease across an epidemiological gradient. These first two goals were developed to help reduce uncertainty for deer managers regarding population impact and recovery of deer from EHD at scales relevant to the MDNR's ability to manage, and where the public perceive changes in deer density due to disease mortality. In Chapter 1 I used rigorous distance sampling estimates at localized scales to compare population abundance and distribution of deer in areas of Michigan that either experienced severe EHD mortality in 2012 or had no historical EHD evidence. My objectives were to 1) test whether I could detect a change in abundance of a deer population attributable to an EHD outbreak in 2012, 2) quantify the finescale spatial extent of EHD impacts associated with riparian habitats and corresponding disease risk for deer populations, and 3) determine if populations increased over time in response to local population impacts from EHD. In Chapter 2 I provided another tool for localized population

assessment using aerial surveys and the novel application of cutting-edge estimation techniques. Specifically, the goal of this study was to evaluate an N-mixture model applied to an aerial survey of unmarked, free-ranging white-tailed deer in an area known to have been affected by EHD-related mortality. Using aerial surveys and a simultaneous data collection approach, the objectives for this chapter were 1) to compare detection and abundance parameters estimated from N-mixture models and distance sampling methods and 2) to test the sensitivity of the spatial unit size inherent in the study design to the N-mixture approach. Developing and applying practical estimation tools for local populations will help managers better assess impacts attributable to disease.

At landscape scales, where environmental or landscape factors may drive the occurrence of EHD in deer in non-endemic regions more broadly, our goal was to better understand recent landscape-level patterns of EHD and anticipate future disease outbreaks in emergent zones. In Chapter 3 I used a longitudinal survey of hemorrhagic disease across the eastern United States for a 15-year period in which disease occurrence has increased (Nettles et al. 1992, Stallknecht et al. 2015). Specifically, I evaluated spatial models for hemorrhagic disease that included drought and related landscape factors predicted to affect disease occurrence through mechanisms affecting the disease vector. My objectives were to 1) develop a spatiotemporal model to evaluate if drought severity and related environmental variables explain changing patterns of HD presence; and 2) to determine if this potential risk factor varies in importance over the present range of HD in the eastern United States. Finally, the epilogue provides a summary of my findings and general conclusions for research and management of emergent EHD.

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CHAPTER 1: EPIZOOTIC HEMORRHAGIC DISEASE AFFECTS ABUNDANCE AND DISTRIBUTION OF FREE-RANGING DEER POPULATIONS

INTRODUCTION

Hemorrhagic disease (HD) is the most significant source of viral disease-related mortality in white-tailed deer (Odocoileus virginianus) in the United States (Howerth et al. 2001). An increase in the frequency and distribution of reported HD in white-tailed deer has occurred across northern latitudes in the Midwest and eastern United States since 1980 (Stallknecht et al. 2015). In particular, the emergence of the HD serogroup epizootic hemorrhagic disease virus (EHDV) has resulted in severe clinical disease and localized mortality of white-tailed deer in the northern range of the disease where deer are immunologically naive (Howerth et al. 2001, Gaydos et al. 2004). Epizootic hemorrhagic disease (EHD), the disease caused by EHDV, is considered endemic in the southeastern US, where infection rates are high but mortality and morbidity are low (Stallknect et al. 1996). However, where outbreaks have been severe in the north, resulting in hundreds or thousands of deer mortalities, the impacts of EHD on deer populations are often unknown and difficult to assess. In these incursive and epidemic zones of disease emergence, the effects of EHD on the population ecology of white-tailed deer are poorly understood (Ruder et al. 2015). There is a clear need to better understand the population-level impacts of EHD in these epidemic zones.

Understanding the impact of epidemic and emerging infectious disease on wildlife populations is crucial for conservation and management as disease outbreaks intensify and spread spatially (Harvell et al. 2002, Ostfeld et al. 2005). However, knowing the extent and population-level impact of emergent wildlife diseases is challenging. In captive white-tailed deer

herds where animals are monitored extensively and the spatial extent of the herd is defined, disease mortality can often be more easily assessed than in free-ranging herds. For example, 46% average herd mortality was documented in captive herds after an EHD outbreak in 2012, which is much higher than any free-ranging deer mortality reports (Stevens et al. 2015). While limited studies exist of EHD-related mortality in free-ranging populations, evidence has shown EHD outbreaks may reduce deer population abundance at least 20%, with more severe reductions where the disease occurs in immunologically naïve deer populations (Gaydos et al. 2004). The immunological response to EHD is related to the history and frequency of past disease outbreaks. This is in part explained by the proportion of EHDV naive animals within a population and the subsequent ability for animals to develop neutralizing antibodies and acquire nearly life-long resistance after exposure (Stallknect et al. 1991, Stallknecht et al. 1996, Coleman et al. 2001, Howerth et al. 2001, Gaydos et al. 2002). Typically, the turnover rate of a deer population is faster than the average periodicity of EHD outbreaks in epidemic zones, leaving a small percentage of the population with immunity to the pathogen and a large susceptible population at the time of the next outbreak. If these patterns persist, deer populations may be prone to continued die-offs given optimal environmental conditions for disease transmission. Over time, deer populations will recover as reproduction continues and new susceptible deer are born or immigrate into an affected area. However, recovery time will be confounded by the maintenance of seroprevalence within the population if disease outbreaks continue (Park et al. 2013). This pattern has been shown at broad scales with HD in the US (Park et al. 2013). However, localized spatio-temporal patterns of EHD impacts on deer populations have not been well studied in epidemic regions of EHD (Gaydos et al. 2004).

EHD is vector-borne and is reliant on the presence and persistence of a vector species capable of transmitting the virus to the deer. The vector, an adult biting midge in the genus *Culicoides*, transmits EHDV in the late summer across the range of the disease and is tied closely to climate conditions and available water for life cycle completion (Shope et al. 1960, Mellor et al. 2000). The effect of EHD on deer populations tends to be localized and often is associated with features such as wetlands or other sources of water where *Culicoides* are found (Davidson 2006). Consequently, the population ecology and distribution of the vector plays a significant role in the epidemiology of hemorrhagic diseases (Mellor et al. 2000, Wilson and Mellor 2008, Savini et al. 2011). HD reports are often associated with warm temperatures and features such as wetlands or other sources of water suitable for the life cycle of the vector species (Davidson 2006, Berry et al. 2012, Xu et al. 2012). While the specific species responsible for EHDV infection in the northern and eastern United States is unclear, we do know that *Culicoides* require similar wetland habitats where disease risk is thought to be greater for deer through increased virus transmission (Ruder et al. 2015). To our knowledge, no study has identified the spatial extent from a wetland at which deer population impacts occur.

Given the temporal and spatial variability of EHD impacts on deer, assessing population parameters in the context of an EHD outbreak is one way in which disease impacts on deer populations may be disentangled. The few studies that have quantified EHD mortality rates or population impacts have relied on opportunistically radio-collared animals or modeling population indices at deer management unit scales (Fischer et al. 1995, Beringer et al. 2000, Gaydos et al. 2004). In the absence of marked animals, Fischer and colleagues (1995) and Gaydos and colleagues (2004) used population metrics from harvest data at the deer management unit scale, in conjunction with disease reports, to estimate white-tailed deer mortality rates in

Missouri and West Virginia, respectively. However, harvest-based population models at the scale of deer management units (e.g., ~2,000 km²) have limitations for assessing disease impacts. This limitation is especially true for the highly localized mortality patterns of EHD, as traditional deer management units would tend to average local population fluctuations across the unit. Linking the scale of the environmental process with the scale of appropriate management action is important for effective regulation and maintenance of the resource (Cumming et al. 2006). Therefore, estimating the impact of EHD on white-tailed deer populations would be best done at a local scale relevant to the ecology and population impacts of the disease.

Increased frequency and intensity of EHD-related deer mortalities on the Michigan landscape since 2006 has generated concern from the public and the Michigan Department of Natural Resources (MDNR) regarding the effects of EHD on local deer populations. In 2012, EHD was confirmed in 30 Michigan counties and mortalities were reported in 21 other counties resulting in approximately 15,000 EHD suspected deer mortalities (MDNR). The first cases of EHD in Michigan occurred late summer of 1955, appearing in four counties across the central lower peninsula of the state (Shope et al. 1960). Another outbreak occurred in 1974 in 5 counties in Michigan, and did not reappear until 2006, when it was found in a single county in the southwest portion of the state (MDNR). Since 2006, EHD was confirmed in 2008-2013, with 2012 being the largest known outbreak (MDNR). Large numbers of dead deer were confirmed to have died from EHDV through laboratory virus isolation in 2012, although not all deer were tested and EHD cases were likely underreported (MDNR). The spatial distribution and relative intensity at which a deer population is affected by EHD is particularly concerning as the sudden reduction in deer abundance may have long lasting effects at local scales.

Due to the emergent nature of this disease in similar northern latitudes over the last 10 years and the expected relationship with midge habitats, there is a clear need for information on localized population impacts of the disease on deer. Our objectives were to 1) test whether I would detect a change in abundance of a deer population attributable to an EHD outbreak, 2) quantify the fine-scale spatial extent of EHD impacts on deer populations associated with riparian habitats and corresponding disease risk, and 3) determine if populations increased over time in response to local population impacts from EHD. I hypothesized that EHD has localized population impacts on white-tailed deer and that those impacts are habitat dependent. Previous research investigating habitat use of deer in agriculture-forest systems has shown that deer select for lowland deciduous-forest cover, often associated with wetlands (Hiller et al. 2009). Thus, deer abundance in a healthy population (as defined by an absence of EHD outbreaks) should have greater local abundance in forested and wetland areas compared to adjacent agricultural areas with limited forest cover. However, in an EHD impacted region, deer associated with wetlands would be more susceptible to disease-related mortality. If that mortality was severe, and abundance is assessed with sufficient precision and at appropriate scales, local population abundance of deer should be lower in forested wetland areas compared to adjacent areas dominated by agriculture.

STUDY AREA

Two study areas in southern Michigan were selected for a natural case-control comparison based on past disease occurrence, landscape metrics relevant to the disease process, and deer abundance. Deer hunting occurred every fall in both study areas and deer harvest regulations were similar between study areas. The Maple River study area (190 km²) within Montcalm, Ionia, Clinton, and Gratiot counties in Michigan, USA was the site of a major deer

mortality event due to EHD in 2012 and served as our case study site (Fig. 1.1 and Appendix A). This study area had notable EHD mortality reports in 2012 with Ionia county reporting 2,498, Montcalm county reporting 910, Clinton county reporting 514, and Gratiot county reporting 319 EHD deer mortalities during the outbreak period (July – October, MDNR unpublished data). Buck harvest, an index of county-level deer abundance prior to data collection, was 2,871, 2,614, 3,400, and 6,442 for Ionia, Clinton, Gratiot, and Montcalm counties, respectively for 2012. This area is in the Lansing loamy plain ecoregion characterized by a flat landscape supporting a mix of forest cover and agriculture consisting primarily of soybeans, grain, corn, and fragmented woodlots. Greater forest cover and water exist near the riparian corridor of the Maple River. The climate has large seasonal variation in temperatures ranging from an average low of -10 degrees C to an average high of 28 degrees C, with 90.42 cm of average annual precipitation.

The Cass River study area (203 km²) lies within Tuscola, Sanilac, and Huron counties in Michigan USA and is similar to the Maple River area in land cover composition and climate (Fig. 1.2). The area is in the Maumee Lake plain ecoregion and dominated by corn, grain, and soy-based agriculture beyond the riparian corridor. Although a total of 8 EHD deer mortalities were reported for Tuscola and Sanilac counties in 2012, none were reported in townships within our study area and none were reported for Huron county, making this site likely EHD-free. The buck harvest for Tuscola and Sanilac and Huron counties in 2012 was 4,619, 6,312, and 3,942 respectively. The climate is slightly less variable than in the Maple River study site, with temperatures ranging from an average low of 1.7 degrees C to 13.3 degrees C, with 85.69 cm of average annual precipitation.



Figure 1.1 The location of line transects used to estimate fine-scale deer abundance at varying distances from a riparian corridor in two study areas in Michigan, from 2013-2016. The Maple River area (red transects) had previously reported severe EHD outbreaks (case site) and the Cass River area (black transects) had no record of past EHD outbreaks (control site).

METHODS

Data collection and study design

To evaluate the role of EHD mortality specifically on local deer abundance and test our ability to estimate abundance at scales relevant to EHD, I surveyed populations at both the EHD-affected site and the EHD-free site. To detect heterogeneity and change in abundance of white-tailed deer at scales relevant to EHD within each site, I designed our study to assess deer abundance within localized habitat arrangements adjacent to riparian areas and in years following a documented disease outbreak (MDNR 2014). I used line-transect distance sampling to estimate deer

abundance for each stratum within each site (Thomas et al. 2010). I placed 2 line-transects within approximately 1 km of the river, and 2 line-transects approximately 5km from the river (Fig 1.1). Survey routes were approximately 24 km long line-transects positioned along low-intensity dirt roads in an adjusted zig-zag pattern (Marques et al. 2001), following a major river corridor within the study area. The observers made counts of deer from motor vehicles to allow for observer detection across maximum distances and habitats. Observers maintained a speed that would ensure that deer were not double counted if running but slow enough to ensure optimal detection of deer along the transect (~20 km/h; Zamboni et al. 2015). The high proportion of private landownership and lack of accessibility for non-motorized vehicles made random transect placement impractical in this study. I selected roads for line-transects based on characteristics that minimized the potential of a negative behavioral response by deer across open agricultural landscapes (Meisingset et al. 2014). All transects were tested for driving conditions and visibility prior to survey initiation. Transects were then surveyed during a time period in which the population could be assumed closed, after fawning (mid-June) season and before hunting (mid-September) season between 2013-2016 for the Maple River study area and 2014-2016 for the Cass River study area. Further, movement of white-tailed deer resulting in population change through immigration and emigration was assumed to be minimal during this period (Long et al. 2008). Low deer density may result in fewer deer available for detection; thus I expected low detection probabilities in the stratum that had recently experienced the greatest disease mortality. Subsequently, survey replicates were increased in these areas to ensure an appropriate sample size and encounter rate. The line-transects were grouped as habitat-based strata in each study area, with each stratum encompassing 1 of the 2 dominant habitat types associated with proximity to a riparian corridor, hereon designated as "wetland" and "agriculture" strata. The

total area for estimation was calculated by creating a 1000 m buffer around each line-transect, and pooling similar habitat types. The agricultural stratum in the Maple River study area was surveyed 6 times in 2013, 8 times in 2014, 8 times in 2015, and 7 times in 2016. The wetland stratum in the Maple River study area was surveyed 8 times in 2013, 10 times in 2014, 10 times in 2015, and 9 times in 2016. The Cass River study area also contained 2 habitat-based stratum, agricultural and wetland, which were surveyed 6 times each in 2014 and 2015, and 8 times each in 2016. Evening surveys were completed within a 3-hour time period and were conducted once per week throughout the data collection period for replication. Finally, line-transects were placed approximately 3 km from each other or were separated by a geographical barrier (large river) to maintain independence between transects at each site.

Free-ranging unmarked deer were counted through ground-based observations on both sides of the transect line beginning within 3 hours prior to sunset and concluding when the survey route was complete or when it was too dark to detect deer. Assuming a minimum number of 2 observers per line-transect were present, all transects in a study area were surveyed simultaneously on a given night. Deer observations were measured with range finders to obtain measures of distance from observers to solitary deer or to the center of a group of deer. A group was defined as deer within approximately 6m of each other. The unit of observation was the deer group to ensure independence in the analyses (Buckland et al. 2001, Lovely et al. 2013). The use of range finders was important to meet the assumption of accuracy in distance measurements. A team of 2-4 observers, including the vehicle driver, searched ahead and perpendicular to the vehicle, stopping the vehicle to use binoculars to verify detection of deer. Direction of travel was alternated among replicate survey days for a given transect to account for potential differences in detection by time of day. Observations of deer or groups of deer were made or confirmed with

10x30 binoculars or unimpeded eye only (no spotlights or thermal imagery were used). If the observer was not perpendicular to the deer observation, a radial angle measurement was taken from the vehicle with a planar protracting device fitted perpendicularly along the vehicle window. Data related to the detection process were collected, including group size, vegetation type (row crop, pasture, forest, residential, other), behavior upon detection (bedded, standing, feeding, moving), observer (biologist or non-biologist team), and sky condition (clear skies, cloudy, light precipitation, fog). Time of day, distance along the transect, location coordinates, and total transect effort were also collected for analysis purposes. Driving conditions were recorded, with conditions of excessive precipitation, fog, or thunderstorms precluded from survey nights. Surveys were coordinated with the Michigan Department of Natural Resources (MDNR), volunteers from local deer-hunting organizations, and students. Observers were categorized as either biologists or not. Regardless of experience, all observers were trained prior to conducting surveys, and protocol was reiterated prior to each survey to ensure consistent data collection. Because an underlying assumption of distance sampling requires that all objects that occur on the line-transect (at distance zero) are detected, I repeatedly instructed all observers to ensure that no objects on or directly adjacent to the line transect were missed. Surveys were not conducted more than once in a 24-hour period as to avoid double counting and maintain independence.

Distance sampling analysis

I analyzed data with conventional distance sampling and multiple covariate distance sampling engines in Program Distance v. 6.2 as described by Thomas et al. (2010). I analyzed data for each stratum in each study area and each year independently using the Program Distance data filter settings, as detection was not assumed homogeneous across years or strata (Buckland

et al. 2009). After conducting exploratory analyses, I truncated all data beyond 450 meters for all transects in all years for improved model fit (Buckland et al. 2001, Williams and Thomas 2007) and for consistency in population inference at a fine-scale across years. I modeled the detection probability function following recommendations of Buckland et al. (2001) and considered variables that were predicted to influence the detection process for each stratum and year but that were not highly correlated with distance from the transect line. I evaluated half-normal and hazard-rate key functions in a step-wise approach and used appropriate expansion terms (cosine or polynomial) provided by Buckland et al. (2001) in combination with up to 3 adjustment terms. Key functions and adjustment terms were selected for each stratum and evaluated with Akaike Information Criterion (AIC) to select the most parsimonious model which best explained detection probability (Burnham and Anderson 2002). I used program DISTANCE to select the appropriate adjustment terms based on minimum AIC for either half-normal or hazard rate key functions with a cosine series expansion (Buckland et al. 2001). Further, I then determined the best cut points for distance intervals from the transect, given the covariates, using goodness-of-fit testing of observed and expected values. Once the most robust key function for the data was identified, I systematically began including covariates in the MCDS engine and bootstrapped the variance when appropriate (e.g., cluster size; Buckland et al. 2001). The covariates used in our model set were coded as factors in the MCDS analysis and included observer team (Obs), weather conditions (Skycode), habitat (Veg), behavior of deer upon detection (Behave), and the group size of the observed deer group (Cluster). For the purposes of analysis, the initial deer detection for an individual or group made by an observer was assigned the appropriate covariate information. Each variable was modeled individually and as a combination of potential interactions developed with an *a priori* model set and implemented with the model definition

properties (Table 1.1). This suit of multivariate models was then evaluated with AIC to select the most parsimonious detection probability model for each year and stratum, assuming model convergence. Of the best models, I assessed the diagnostic histograms, qq-plots, and the % coefficient of variation to ensure our data met the assumptions of distance sampling and parameter estimates had adequate precision needed for population inferences. I evaluated Kolmogorov-Smirnov goodness-of-fit to further verify models selected as the most likely to fit the data (Buckland et al. 2004). Once the model with greatest likelihood was selected for each stratum in each year, I estimated abundance, detection probability, and variance associated with point-estimates. I derived density by dividing the abundance estimate by the respective stratum area. Because our desired level of inference was at the stratum level within each study site, indicating the recent spatial distribution of disease mortality impacts, I did not attempt to combine estimates for the entire study area.

Table 1.1 Notation and description for a priori distance sampling models for estimating
abundance and density estimates of white-tailed deer in the Maple River and Cass River study
areas of Michigan, 2013-2016.

Detection Variables	Description				
Cluster	The number of deer counted within a group				
Sky	Weather condition on the given survey night (clear, partly cloudy, overcast, fog, light rain)				
Veg	Habitat cover (Row crop, pasture, forest, residential, other)				
Obs	Observer team; inclusion of a biologist or not				
Behave	Behavior of deer upon initial detection (running, walking, standing, feeding, bedded)				
Cluster + Behave	Interaction between deer group size and deer behavior				
Cluster + Obs	Interaction between deer group size and detection by observer				
Cluster + Sky	Interaction between deer group size and weather conditions during survey				
Null	Hazard rate or Half-normal key function only (depending on minimum AIC)				

RESULTS

Data collection

Our total survey effort was 3,323 km in our EHD site (Maple River study area) over the course of 4 summers (2013-2016), and 1,993 km in our control site (Cass River study area) over the course of 3 summers (2014-2016). Surveys resulted in a total of 1,481 observations and 2,725 observations in the EHD site and the control site, respectively, with observations being a single deer or a group of deer within approximately 6m of each other. This group classification was similar to Lovely et al. (2013) distance sampling protocol of white-tailed deer in Virginia and based on prior group size research of white-tailed deer (Lagory 1986). The range of mean group (or Cluster) size for the EHD site across years was 1.69 - 2.69 (SE = 0.09 - 0.21) deer and was 2.29 - 2.98 (SE = 0.11 - 0.16) deer for the control site. However, because the expected group size occasionally suggested size bias, I used the size-bias cluster estimation method for the deer density and abundance parameter estimation.

Model selection

The half-normal key function was selected using minimum AIC for all except 2 years in a single stratum when the hazard-rate key function was selected (agriculture stratum in EHD site 2015 and wetland stratum in control site 2015) (Table 1.2). After conducting exploratory analysis and testing models for convergence, the habitat type covariate was removed from further model evaluation as a variable that may affect detection function estimation due to high correlation with distance from the transect line. Habitat type has often been cited as an important predictor of detection functions for deer (Lovely et al. 2013, Zamboni et al. 2015), but model convergence rarely occurred when the habitat covariate was included and correlation issues were

apparent relative to distance and habitat composition associated with transect lines (low-intensity roads). The models that garnered the highest support from the data with minimum AIC criteria, provided reliable model convergence, and best explained the variance in detection probability included covariates for group size or deer behavior, but varied by year, study area, and stratum (Table 1.2). The weather condition variable (skycode) was important in 2016 for describing the variance in detection for the agriculture stratum in both study areas, and the wetland stratum for Maple River in 2015 (Table 1.2). No other covariates were selected using AIC, indicating observer effects were not present in our data (Table 1.2).

					GOF K-	ESW (est.		
			Model; Key function and No.		Sp-	strip	Tot. No.	
Year	Study Area	Stratum	adjustment terms	k	value	width)	observations	Tot. Effort
			Cluster + Behave; Half-normal,					
2014	Cass River	Ag	0	5	0.0804	323.49	286	181.8
		U	Cluster + Behave; Half-normal,					
2014	Cass River	Wetland	0	5	0.2396	311.08	416	186.9
2015	Cass River	Ag	Cluster; Half-normal, 0	3	0.1734	259.78	396	191.6
2015	Cass River	Wetland	Cluster; Hazard-rate, 2	5	0.2416	373.9	572	180
2016	Cass River	Ag	Clust + Skycode; Half-normal, 3	6	0.06	306.52	479	241.9
2016	Cass River	Wetland	Clust + Behave; Half-normal, 3	9	0.1911	298.95	576	256
2013	Maple River	Ag	Behavior: Half-normal, 0	4	0.792	273.45	83	171.1
2013	Maple River	Wetland	Behavior: Half-normal, 0		0.0152	192.96	59	227.3
	1		Cluster + Behave: Half-normal					
2014	Maple River	Aσ	0	5	0.5838	306.65	251	245.8
2014	Maple River	Wetland	Cluster: Half-normal, 0	2	0.7168	290.37	170	309.4
	.1		Cluster: Hazard-rate Simple					
2015	Maple River	Ασ	poly 0	3	0 1 1 8	260 72	229	246.4
2015	Maple River	Wetland	Clust + Skycode: Half-normal 0	4	0.0404	304 51	185	313
2015	inapie iniver	or chante	chuse - brycoue, man norman, o	т	0.0404	504.51	105	515
2016	Maple River	Δσ	Clust + Skycode: Half-normal 0	5	0 1638	298.16	259	240.8
2016	Maple River	Wetland	Clust + Behave: Half-normal 0	7	0.142	235.63	245	311.2
	Year 2014 2014 2015 2015 2016 2016 2013 2013 2013 2014 2014 2015 2015 2016 2016	YearStudy Area2014Cass River2014Cass River2014Cass River2015Cass River2015Cass River2016Cass River2016Cass River2013Maple River2014Maple River2015Maple River2015Maple River2016Maple River2015Maple River2015Maple River2016Maple River2016Maple River2016Maple River	YearStudy AreaStratum2014Cass RiverAg2014Cass RiverWetland2015Cass RiverAg2015Cass RiverAg2016Cass RiverAg2016Cass RiverAg2013Maple RiverAg2014Maple RiverAg2015Maple RiverAg2014Maple RiverAg2015Maple RiverAg2016Maple RiverAg2015Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg2016Maple RiverAg	YearStudy AreaStratumModel; Key function and No. adjustment terms2014Cass RiverAgO Cluster + Behave; Half-normal, O Cluster + Behave; Half-normal, O2014Cass RiverWetlandO2015Cass RiverAgCluster; Half-normal, O Cluster; Half-normal, O2015Cass RiverAgCluster; Half-normal, O Cluster; Hazard-rate, 22016Cass RiverAgClust + Skycode; Half-normal, 3 Clust + Behave; Half-normal, 32013Maple RiverAgBehavior; Half-normal, O Cluster + Behave; Half-normal, 0 Cluster + Behave; Half-normal, 0 Cluster + Behave; Half-normal, 0 Cluster; Hazard-rate Simple2014Maple RiverAgO Cluster; Hazard-rate Simple2015Maple RiverAg WetlandO Cluster; Hazard-rate Simple2015Maple RiverAg WetlandO Clust + Skycode; Half-normal, 0 Clust + Skycode; Half-normal, 02016Maple RiverAg WetlandO Clust + Skycode; Half-normal, 0 Clust + Skycode; Half-normal, 02016Maple RiverAg WetlandClust + Skycode; Half-normal, 0 Clust + Skycode; Half-normal, 02016Maple RiverAg WetlandClust + Skycode; Half-normal, 0 Clust + Skycode; Half-normal, 0	YearStudy AreaStratumModel; Key function and No. adjustment termsk2014Cass RiverAgCluster + Behave; Half-normal, 052014Cass RiverWetland052015Cass RiverWetland052015Cass RiverAgCluster; Half-normal, 032015Cass RiverWetlandCluster; Hazard-rate, 252016Cass RiverAgCluster; Hazard-rate, 252016Cass RiverAgClust + Skycode; Half-normal, 362013Maple RiverAgBehavior; Half-normal, 042013Maple RiverAgCluster; Half-normal, 032014Maple RiverAgCluster; Half-normal, 032015Maple RiverAgO52015Maple RiverAgO32015Maple RiverAgO32015Maple RiverAgpoly, 032016Maple RiverAgClust + Skycode; Half-normal, 042016Maple RiverAgClust + Skycode; Half-normal, 042016Maple RiverAgClust + Skycode; Half-normal, 042016Maple RiverAgClust + Skycode; Half-normal, 072016Maple RiverAgClust + Skycode; Half-normal, 07	GOF K- Sp- Adjustment termsGOF K- Sp- k valueYearStudy AreaStratumModel; Key function and No. adjustment termsSp- kvalue2014Cass RiverAgCluster + Behave; Half-normal, 050.0804 Cluster + Behave; Half-normal,2014Cass RiverWetland050.23962015Cass RiverAgCluster; Half-normal, 030.1734 20152016Cass RiverMetlandCluster; Hazard-rate, 250.24162016Cass RiverAgClust + Skycode; Half-normal, 360.06 20162013Maple RiverAgBehavior; Half-normal, 040.792 20132013Maple RiverAgBehavior; Half-normal, 030.0152 20152014Maple RiverAgO50.5838 20142015Maple RiverAgO30.118 20152015Maple RiverAgCluster; Half-normal, 030.118 20162016Maple RiverAgO30.118 20142016Maple RiverAgClust + Skycode; Half-normal, 040.04042016Maple RiverAgClust + Skycode; Half-normal, 050.1638 20162016Maple RiverAgClust + Skycode; Half-normal, 050.1638 20162016Maple RiverAgClust + Skycode; Half-normal, 070.142	YearStudy AreaStratumModel; Key function and No. adjustment termsGOF K- S p- valueESW (est. S p- width)2014Cass RiverAgCluster + Behave; Half-normal, 050.0804323.492014Cass RiverWetland050.2396311.082015Cass RiverMgCluster; Half-normal, 030.1734259.782015Cass RiverWetlandCluster; Half-normal, 030.1734259.782015Cass RiverWetlandCluster; Hazard-rate, 250.2416373.92016Cass RiverAgClust + Skycode; Half-normal, 360.06306.522013Maple RiverAgBehavior; Half-normal, 030.0152192.962014Maple RiverAgO50.5838306.652014Maple RiverAgO50.5838306.652014Maple RiverAgO30.118260.722015Maple RiverAgpoly, 030.118260.722015Maple RiverAgClust + Skycode; Half-normal, 040.0404304.512016Maple RiverAgClust + Skycode; Half-normal, 040.0404304.512015Maple RiverAgClust + Skycode; Half-normal, 040.0404304.512015Maple RiverAgClust + Skycode; Half-normal, 040.0404304.512016M	YearStudy AreaStratumModel; Key function and No. adjustment termsGOF K- stripESW (est. strip2014Cass RiverAg 0050.0804323.492862014Cass RiverWetland050.2396311.084162015Cass RiverWetland050.2396311.084162015Cass RiverAg WetlandCluster; Half-normal, 030.1734259.783962015Cass RiverAg WetlandCluster; Half-normal, 030.1734259.783962016Cass RiverAg WetlandCluster; Hazard-rate, 250.2416373.95722016Cass RiverAg WetlandClust + Skycode; Half-normal, 360.06306.524792016Cass RiverAg WetlandClust + Behave; Half-normal, 390.1911298.955762013Maple RiverAg Behavior; Half-normal, 030.0152192.96592014Maple RiverAg Ultart Hehave; Half-normal, 030.0152192.96592014Maple RiverAg WetlandCluster; Half-normal, 020.7168290.371702015Maple RiverAg WetlandClust + Skycode; Half-normal, 030.118260.722292015Maple RiverAg WetlandClust + Skycode; Half-normal, 040.0404304.511852016Maple

Table 1.2 Models selected for each stratum in each year and corresponding selection criteria and data descriptors.

Deer density and abundance estimates

The best model for each year and stratum based on the minimum AIC and model fit criteria was used to estimate a detection function that was specific for annual deer population abundance and density estimates and associated 95% confidence intervals in each stratum (Table 1.2, Fig. 1.2). All estimates had sufficient minimum observations as recommended by Buckland et al. (2001) and met goodness-of-fit criteria and detection function fit criteria (Table 1.2-1.3, Appendix B). In the EHD affected area, I found deer abundance was significantly higher in the agricultural stratum in 2013 (281; CI: 165-401) and 2014 (220; CI: 151.18-301.79) than in the wetland stratum for 2013 (60; CI: 42.52-78.7) and 2014 (107; CI: 92.59-133.25). Further, deer population density estimates were lowest in the wetland stratum of the EHD site for all years compared to either stratum in the unaffected study area, including the minimum density estimate (Fig. 1.3; 0.63; CI: 0.44-0.82 in 2013 affected area vs. 8.94; CI: 6.68-11.66 in 2014 unaffected area). I found the wetland stratum in the EHD site was the only stratum to experience consistent population increases over the course of the 4 year study, with abundance estimates doubling in 2016 compared to 2013 (Table 1.3, Fig. 1.3). Population abundance in the control site (Cass River study area) did not change over time (Fig. 1.4). Further, the wetland stratum was not different from the agricultural stratum except in 2014, when deer density was greater in wetland habitat (580.39; 95% confidence interval (CI): 539.31-628.80) than in the agriculture habitat (344.68; 95% confidence interval (CI): 257.33-449.30).

				Estimate	N 959	%CI*	N 95%CI*			N 95% CI*		
	G. 1		Total area							D		
V	Study	C.	$(km.^2)$ of	A 1 1	LCI	UCI		LCI	UCI	Detection	LOI	UCI
Year	Area	Stratum	estimation	Abundance	LCI	UCI	Density	LCI	UCI	Prob.	LCI	UCI
2014	Cass River	Ag	99.82	344.68	257.33	449.30	3.45	2.58	4.50	0.72	0.67	0.77
	Cass											
2014	River	Wetland	103.6	580.39	539.31	628.80	5.60	5.21	6.07	0.69	0.65	0.73
	Cass											
2015	River Cass	Ag	99.82	532.00	371.26	695.99	5.14	3.59	6.72	0.58	0.54	0.62
2015	River Cass	Wetland	103.6	577.76	516.32	854.37	5.58	4.99	8.25	0.83	0.79	0.88
2016	River	Ag	99.82	458.10	364.98	532.38	4.59	3.66	5.34	0.68	0.65	0.72
2016	Cass	Watland	102.6	560 54	460.20	661 20	5 50	4 4 4	6 20	0.66	0.62	0.70
2010	Magla	wettand	105.0	309.34	400.29	001.38	3.30	4.44	0.39	0.00	0.05	0.70
2013	River	Ag	94.07	280.68	165.00	401.00	1.49	0.88	2.13	0.61	0.52	0.71
	Maple											
2013	River	Wetland	95.86	60.24	42.52	78.7	0.63	0.44	0.82	0.46	0.38	0.56
2014	Maple River	Aσ	94.07	219.98	151.18	301.79	2.34	1.61	3.21	0.68	0.63	0.74
	Maple	8	2									
2014	River	Wetland	95.86	106.62	92.59	133.25	1.11	0.97	1.39	0.65	0.58	0.71
2015	River	Ag	94.07	184.96	109.56	250.92	1.97	1.17	2.67	0.58	0.53	0.63
	Maple											
2015	River Maple	Wetland	95.86	125.53	105.25	169.16	1.31	1.10	1.77	0.68	0.62	0.74
2016	River	Ag	94.07	210.53	124.86	306.61	2.24	1.33	3.26	0.66	0.60	0.71
2016	Maple	Wetley 1	05.94	206.07	170 54	252 52	2.15	1.96	2.64	0.52	0 47	0.50
2016	River	wetland	95.86	206.07	1/8.54	252.53	2.15	1.86	2.64	0.52	0.4/	0.59

Table 1.3 Parameter estimates from best fitting models in each stratum, study area, and year for 2013-2016 in Michigan. Asterisks represent 95% confidence intervals from bootstrapping.



Figure 1.2 Deer density and 95% confidence interval estimates (deer/sq. km) and for the Maple River study area (EHD site) for 2013-2016 in Michigan.


Figure 1.3. Deer density and 95% confidence interval estimates (deer/sq. km) and for the Cass River study area (control site) for 2014-2016 in Michigan.

DISCUSSION

Understanding the spatial and temporal dynamics of emerging epizootic hemorrhagic disease in northern latitudes is becoming increasingly important for wildlife conservation and management. Disentangling these impacts across space and time as the disease expands northward is complicated by variation in host infection rates, spatiotemporal host immunity patterns, vector dynamics, reporting and sampling bias, and host population dynamics. (Stallknecht et al. 2015, Ruder et al. 2015). Our findings show that I could detect differences in the population distribution of deer within 1 km from a riparian corridor of known EHD occurrence in 2012 compared to a population only 5 km from the same riparian corridor, with reduced abundance nearest the river. In the control site there was no difference in deer population over time or at varying distance from the riparian corridor. Importantly, the local deer population most affected by EHD was the only population in our study that had a consistent and measurable population increases across the 4 subsequent years following an EHD outbreak. These findings lead us to conclude that EHD was the driving force behind the population changes I detected in the riparian corridor of Maple River. To our knowledge, this is the first study to provide empirical evidence that EHD has fine-scale population impacts on white tailed deer, and those impacts are habitat dependent.

My findings suggest that epizootic hemorrhagic disease had significant impacts on the deer population in the riparian corridor of the Maple River study area. Populations in this area were perceived to have been heavily impacted by the 2012 outbreak due to large numbers of dead deer observed and reported during the 2012 outbreak. Within the same affected study area, I found an increase in deer abundance from the summer of 2013 to 2016 in the wetland stratum nearest the riparian corridor were EHD had been most severe in a 2012 outbreak, and slightly

higher deer density, but with no population change, for populations measured farther from the riparian corridor (within 5km) (Fig. 1.3). Further, there was no change in deer density, with greater variation and higher overall density estimates, in the two stratum with no past EHD report history (Fig. 1.4). In the stratum nearest the riparian corridor in the control site, mean deer densities were higher, which corresponded with predictions for increased deer habitat selection and absence of EHD impacts for this area. Our research suggests that localized EHD mortality was the driving force behind the observed population variation and subsequent population change in two otherwise comparable landscapes.

EHD outbreaks have long been assumed to be spatially localized, but only a few previous studies have attempted to explicitly quantify the distribution and spatial scale of an outbreak for free-ranging deer at a population level (Fischer et al. 1995, Gaydos et al. 2004). In our study, the Maple River study area had documented cases of numerous EHD mortalities in 2012 and was likely a completely naive population to EHDV, as the last reported EHD case in the area was in 1974 (MDNR 2012). I detected differences in deer populations associated with riparian corridors and wetlands, which have been found to affect EHD dynamics and in endemic regions (Berry et al. 2013) and are critical for the larval stage of *Culicoides* spp. (Mellor et al. 2000). This localized impact of EHD is likely due to a combination of mechanisms affecting observed mortality in wild deer, including herd immunity dynamics, association of the disease with its vector (*Culicoides*), and reporting of detected animals. The abundance and distribution of Culicoides species capable of transmitting EHDV to deer is a key factor in the presence of EHD across the range of the disease (Mullens et al. 2004, Savini et al. 2011, Ruder et al. 2015). It is likely that the distribution and habitat requirements for the *Culicoides* vector is the limiting factor driving localized EHD impacts on deer in epizootic disease regions.

The differences in deer density between the control site and the EHD site in our study, particularly when comparing the two wetland stratum representing high-quality habitat, provided another indication that EHD mortality in 2012 was driving the observed population variation. Previous research investigating deer habitat use in agricultural-forest landscapes has shown that deer select for forested riparian corridors (Walter et al. 2011), that greater deer densities exist in riparian corridors compared to areas with less riparian habitat (Compton et al. 1988), and that during dispersal movements, deer selectively move within riparian corridors (Clements et al. 2011). Thus, deer abundance in a healthy deer population (as defined by absence of EHD outbreaks in this case) should have greater local abundance in forested areas associated with wetlands compared to mostly agricultural areas lacking forest cover. I found the lowest estimated deer densities across both study areas and all stratum was the wetland stratum nearest the riparian corridor in otherwise highly suitable habitat (Fig. 1.3). This habitat-density pattern was not the case in the wetland habitat of the control site, where deer density was greater than or equal to deer densities in agricultural habitat. Wetland or riparian corridors in agriculture-forest landscapes thus pose increased EHD risk for deer, given the significant reduction of deer density in the EHD affected wetland area of Maple River.

Deer population density increased in a consistent manner across the 4 years of the study in the wetland stratum of the Maple River study area (Fig. 1.3). This was the only stratum that had a consistent upward trajectory for deer abundance and density parameter estimates. I argue that the observed population increase was due to the sudden release of intraspecific competition in a resource abundant habitat due to a severe mortality event from EHD. Assuming EHD mortality did significantly reduce the deer population in this localized area from pre-outbreak densities, deer ecology would predict that maximized recruitment rates likely drove the

population increase observed in our study. For many species, including white-tailed deer, population growth rates are optimized when populations are low due to density dependent mechanisms, which are a function of recruitment relative to population carrying capacity (Milner-Gulland and Akcakaya 2001, McCullough 1979). In K-selected species, the greatest opportunity to observe maximum recruitment per female is shortly after a significant population reduction and subsequent release from intraspecific competition (McCullough 1979). Further, minimal immigration into the population would be expected within the time interval of this study and given the low proportion of dispersing individuals (yearling males) in a white-tailed deer population and the highly philopatric nature of the female portion of the population (Porter et al. 1991).

My findings provide clear spatial distributions associated with EHD impacts at the deer population level and evidence of population recovery where EHD impacts occurred. Populationlevel effects of EHD observed in my study are likely similar to effects on white-tailed deer populations in other epidemic regions of EHD occurrence. Recent patterns of EHD have demonstrated increased frequency and intensity of outbreaks (Stallknecht et al. 2015), resulting in increasing concern over deer resource management and population declines. I demonstrate that while disease impacts may result in significant changes in deer populations, severe mortality will likely remain localized in association with wetland habitats capable of hosting vector populations. Further, deer populations are expected to increase significantly post-outbreak, assuming abundant food resources and limited mortality factors exist over time.

Epizootic hemorrhagic disease is a significant source of non-harvest deer mortality across the geographic range of the disease (Shope et al. 1960, Stallknecht et al. 2015). Although historically a significant disease for white-tailed deer in the Southeastern and Great Plains

regions of the United States, EHD has more recently emerged at increasingly northern latitudes, affecting deer populations at greater frequency and intensity, generating considerable uncertainty regarding the population impacts of the disease on deer (Stallknecht et al. 2015). The emergence of this disease is complex and may have negative consequences for white-tailed deer populations across much of the northern latitudes of the US where deer are currently naïve to EHDV. This study provided information on the scale at which EHD impacts should be addressed, and helped inform expectations for impacts of future outbreaks. If EHD occurrence continues to occur, but at a frequency not conducive for the development of herd immunity at landscape scales, significant mortality events will continue and should be addressed when planning deer management objectives. Further, the collection of consistent seroprevalence data from deer across the emerging range of the disease would provide managers with better information on the susceptibility of deer populations to EHDV and expected mortality impacts.

APPENDICES

APPENDIX A: SUPPLEMENTARY EHD SURVEILLANCE MAP OF DATA REPORTED IN 2012 IN MICHIGAN. MAP PRODUCED BY THE MICHIGAN DEPARTMENT OF NATURAL RESOURCES.

Figure A.1 A map of Epizootic Hemorrhagic Disease occurrence in Michigan 2012.



APPENDIX B: SUPPLEMENTARY DETECTION PROBABILTY HISTOGRAMS FOR

DISTANCE SAMPLING ESTIMATES IN CHAPTER 1.

Figure B.1 Fitted detection probability histograms of deer observations at binned distance intervals for the Cass River and Maple River study areas from 2014-2016 and 2013-2016, respectively, in Michigan.



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LITERATURE CITED

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CHAPTER 2: APPLICATION OF N-MIXTURE MODELS FOR AERIAL SURVEYS OF WILDLIFE: A COMPARISON STUDY

INTRODUCTION

Aerial surveys are often the most practical methods for estimating wildlife population abundance and have been developed to address issues of survey feasibility and reliability of parameter estimates (Caughley 1974, Burnham et al. 1980). Accounting for imperfect detection of abundance is important for obtaining precise and unbiased estimates (Denes et al. 2015). However, methods to account for imperfect detection using aerial surveys are limited and not always practical for wildlife managers. Distance sampling (Buckland et al. 2001) is a wellestablished method for obtaining abundance that allows accounting for imperfect detection, and has been applied to aerial survey approaches numerous times in wildlife research. Unfortunately, this method relies on assumptions that can be difficult to accommodate in aerial surveys. Alternatively, N-mixture models (Royle 2004) are a new analytic tool that have recently been applied to wildlife population estimation (Chandler and King 2011, Zipkin et al. 2014, Lyet et al. 2016, Keever et al. 2017). Similar to distance sampling, N-mixture models explicitly estimate detection probability and abundance, yet have not been applied to aerial surveys of terrestrial free-ranging wildlife to our knowledge. Evaluation of this emerging method is needed in the context of traditional aerial survey methodologies.

Distance sampling has been one of the few methodological options that account for imperfect detection while estimating abundance of unmarked, free-ranging wildlife populations. This method has a long history of use for abundance estimation using count data and distance measurements, and has proven applicable to a wide range of taxa and environments (Buckland et

al. 2004). Distance sampling originated from quadrat and line transect sampling in the early 1900's and was developed further to utilize perpendicular distances (Buckland et al. 2000, Buckland et al. 2001), ultimately resulting in a methodological extension of plot sampling where not all animals are detected within the covered area (Buckland et al. 2010). The framework of distance sampling (Buckland et al. 2001, 2004) typically does not present a fully model-based analysis (i.e. not using a stochastic, non-randomized sample). Rather, the detection function is derived from the observed data, relying on the assumption that detection of animals degrades as distance from the transect line increases and these observations are a randomized sample of the true population (Buckland et. al. 2001). Detection functions can then be calculated and are informative for abundance or density estimates given the spatial extent of the study region. Using this methodology assumes that the population of interest is closed, that distance measurements are accurately collected, and that animals are distributed independently of a survey line or point (Buckland et al. 2001).

Challenges of applying distance sampling in aerial surveys vary in degree and impact on density estimates (White et al. 1989). Among the critical assumptions is that all animals at distance zero are detected with certainty and that animals are detected and measured at their initial location upon detection (Buckland et al. 2001).Violation of this particular assumption results in biasing the density estimate low, which can easily occur in aerial surveys where animals on the line-transect are missed when directly under the aircraft and not otherwise counted or corrected for (Caughley 1974). Further, decisions about appropriate distance intervals or cut-points and assignment of distance interval for observed animals may fail to meet the assumption of accurate distance measurement for detected animals (Buckland et al 2001). Minor shifts in altitude and angle affect distance measurements at ground level taken from a moving

aircraft. If an aerial survey is able to accommodate these assumptions, distance sampling can effectively incorporate model covariates for estimating detection probability and is a useful method for abundance estimation. However, procedures needed to meet these assumptions may be challenging.

N-mixture models are a relatively new approach for estimating abundance and detection processes in wildlife populations (Royle 2004). Like distance sampling, this analytical method explicitly accounts for imperfect detection of sampled animals, but does so using a hierarchical model for detection probability and abundance parameters (Royle 2004). This method appears to be flexible for studies across taxa and for a wide range of ecological questions, allowing the inclusion of habitat covariates, multispecies models, single species models, and estimation of unmarked animals (Kery et al. 2005, Chandler and King 2011, Zipkin et al. 2014, Lyet et al. 2016, Keever et al. 2017). N-mixture models use count data to estimate population abundance and associated detection probabilities for a closed population of interest. These models are a hierarchical extension of a Poisson generalized linear model (GLM) and use temporal replicates of counts that are sampled from multiple independent spatial locations for site-specific abundance (Royle 2004). A principal contribution of this class of models is that the population sizes, N, are specific to each spatial unit (site) and are independent random variables with a mixing distribution. These models combine a binomial generalized linear model (GLM) and a standard model (e.g., Poisson) for N_i (population abundance at site *i*). The observed counts at a unit *i* are assumed to be independent realizations of a binomial process dependent on the detection probability at a given site and time, p_{ij} (the observation process; Kery et al. 2005, Royle 2004). Further, abundance at each site, N_i, has a Poisson or negative binomial distribution, and is a random latent variable specified by parameters in the model as the ecological process

(Denes et al. 2015). The resulting estimated abundance parameters across sites can then generate a posterior estimate of total abundance given some unit of space, which is determined by the study design (Royle 2004). The spatial replication employed in these models and flexibility to incorporate covariates has been shown to produce statistically and ecologically reasonable estimates of abundance (Kery et al. 2005, Joseph et al. 2009).

While N-mixture models are increasingly applied to wildlife populations, they have rarely been applied to aerial surveys for terrestrial wildlife. One study by Lyet and others (2016) estimated abundance of Nile Crocodiles using aerial surveys along the Nile River and N-mixture models. This method was useful for an aquatic obligate available for detection in a spatially discrete water body (Lyet et al. 2016). This research may have been successful in part due to the defined spatial area inherent in the study design for a water body. Spatial unit size selection for N-mixture models is unclear for free-ranging animals with unknown spatial-use boundaries. No previous study has used N-mixture models for aerial surveys of free-ranging terrestrial wildlife and further evaluation is needed to understand the utility of this method for aerial surveys of wildlife. The goal of my study is to evaluate whether N-mixture models could be applied to an aerial survey of unmarked, free-ranging white-tailed deer (Odocoileus virginianus) for localscale population estimation. I seek to simultaneously apply distance sampling and N-mixture models to a multi-year aerial survey of free-ranging deer to make direct comparisons of parameter estimates between analytical methods. In this context, I am interested in designing and specifying distance sampling methods for line-transect sampling approaches (Buckland et al. 2001, Buckland et al. 2004, Thomas et al. 2010), and adapting these line-transect surveys to include data needed for N-mixture models. My specific objectives were to: 1) compare detection and abundance parameters estimated from N-mixture models and distance sampling methods and

2) to test the sensitivity of the spatial unit size inherent in the study design to the N-mixture approach.

STUDY AREA

The Maple River corridor in Montcalm, Ionia and Clinton, and Gratiot counties in south central Michigan was the site of a major deer mortality event due to epizootic hemorrhagic disease (MDNR) in 2012. My study area (190 km²) bisected this corridor and was generally representative of adjacent landscapes (Fig. 1.1). Buck harvest, an index of county-level deer population abundance prior to data collection, was 2,871, 2,614, 3,400, and 6,442 for Ionia, Clinton, Gratiot, and Montcalm counties, respectively for 2012. This area is in the Lansing loamy plain ecoregion characterized by a flat landscape supporting a mix of forest cover and agriculture consisting primarily of soybeans, grain, and corn and fragmented woodlots. Greater forest cover and water exist near the riparian corridor of the Maple River. The landcover composition aggregated across our survey areas included 2.3 % developed land, 70 % forage cropland, 9.7% forest, 1.1% shrubland, 16.3% wetland, and .6% bare ground or other landcover (Fig. 1.1). The climate has large seasonal variation in temperatures ranging from an average low of -10 degrees C to an average high of 28 degrees C, with 90.42 cm of average annual precipitation, including snowfall. The Maple River area had notable EHD mortality reports in 2012 with Ionia county reporting 2,498 EHD deer mortalities and Clinton County reporting 514 EHD deer mortalities during the outbreak period (MDNR report 2014). A related research project established independent deer abundance estimates each summer for this study area in the same time period (Christensen 2017).



Figure 2.1 Aerial survey transects bisecting habitat in the Maple River Study Area of Michigan, USA, 2014-2016.

METHODS

Aerial survey design

I designed an aerial survey protocol to collect data relevant to both distance sampling and N-mixture model methods (Royle 2004). Survey flights were coordinated with Michigan Department of Natural Resources (MDNR) pilots using a fixed-wing aircraft. Deer were surveyed using a double-count approach where observers viewed deer from opposite sides of the aircraft and then repeated the survey in the opposite direction, effectively counting both sides of the transect line twice. We did this by using a line-transect method for distance sampling and including a replicate survey in the opposite direction immediately following the first survey. Observers recorded the location of deer or groups of deer along the transect using a GPS unit, allowing the assignment of deer observations to spatial units (i) needed for analysis with Nmixture models. To standardize the effective survey area of estimation for both methods, we selected a strip width of 900 m that corresponded to a significant decrease in detection probability provided by the collected distance sampling data and graphed in program DISTANCE (Thomas et al. 2010). This value was determined using distance data collected during the flight and was specific to the species and conditions for this survey. Subsequently, the 900 m distance provided a boundary for all spatial units at a distance perpendicular to the transect line. We were interested in population abundance estimates for the covered survey region only and did not extrapolate to a larger study area using traditional distance sampling approaches. We conducted a total of 6 winter surveys, 3 in 2014 and 3 in 2016, that provided data for both analytical frameworks. Each of the 3 surveys in a given year were conducted >24 hours apart to ensure independence between surveys.

We used line-transect distance sampling to estimate deer abundance (Thomas et al. 2010). Transects were selected using a random starting point and were then assigned at standardized distances from that point for a total of 5 north-south transects equally spaced at 4.8km apart and 21 km in length, covering our area of interest. The transect placement was designed to exceed the average size of winter home range for white-tailed deer in a forest-agriculture landscape to ensure we did not count the same deer on multiple transects or spatial units (Hiller et al. 2009). Transects were placed over roads, which were effectively not surveyed because they were not visible under the plane. I placed transects to bisect a major riparian

corridor running southwest to northeast within the study area to sample the deer population across potential habitat-related population density gradients (Marques et al. 2013). Distance intervals were demarcated on the window and strut of the aircraft and were calculated based on guidelines for aerial surveys in Buckland et al. (2001) using relative interval cut-points for line transects. These were 0-100m = A, 101-200m = B, 201-350m = C, 351-500m = D, and 501m-1000m = E. To maintain accurate distance cut-points for each observer, we recalibrated the appropriate angles for the desired intervals for each observer using a clinometer (Buckland et al. 2001). Surveys were consistently flown at near 153m altitude and a flight speed of 167 km/hr for each survey (Caughley 1976), and surveys only occurred when full snow coverage existed for maximum detection of deer.

The same 2 primary observers were maintained in the rear of the plane across years to reduce variation across surveys by individual observer. Both primary observers were focused on a single side of the aircraft when heading in a given direction during the survey. At the completion of a survey pass, the aircraft immediately turned around and the transect was flown in again in the opposite direction so each observer sampled both sides of the transect line once in a survey day, allowing a replicated count in each day. No communication occurred between observers on either side of the plane, but observers were able to communicate with 2 secondary observers (pilot and forward passenger) who were sitting in front of each primary observer and not responsible for collecting data aside from GPS coordinates when requested. Observers collected the perpendicular distance category (distance categories A-E) for each deer observation. Further, observers recorded covariate data of interest for each observation of deer including: the initial observer (front or rear of aircraft), the group size, the activity of the deer at time of observation (bedded, standing, or moving), and the habitat cover type associated with

each recorded observation (wooded, open, or residential). These covariates were included in our analysis.

Distance sampling analysis

We used the conventional distance sampling and multiple covariate distance sampling engines with a line-transect framework in Program Distance v. 6.2 as described by Thomas et al. (2010) to estimate abundance and detection probability parameters. The standard formulation of the population density is given with a function of abundance for a line transect:

$$\widehat{D} = \frac{\widehat{N}}{A} = n/2wL\widehat{P}_a,$$

where constants include A = the size of the region of interest, n = the number of animals or clusters detected, $L = \sum l_j$ where l_j = the length of jth line and j = 1...k (a measure of survey effort) where k is the number of line transects. The truncation distance for measurements from the line is w, and 2w accounts for measurements on both sides of a transect line. \widehat{D} is the estimated density of individuals per unit area (\widehat{N}/A).

The distance sampling method relies on fitting a detection function from observed distances to an object. Distance measurements were collected for each deer observation during the survey, providing a frequency of detections across distances. The detection function, parameter g(x), is estimated by fitting a model to our data. Selecting a key function to select a good model of the true detection function (g(y)) will determine the basic model shape, reflecting the data. This detection function contains the observation process, and assumes a degrading, conditional relationship between detection probability and distance. The most commonly used key functions have the best shape criterion and model robustness and were statistically derived

by Buckland and colleagues (2001). The half-normal and hazard rate are most commonly used, and were evaluated for fit in all of our models. Key functions are important for estimating a detection function given the data and should be evaluated with model selection and visual inspection of distance frequency histograms (Buckland et al. 2001). Appropriate key functions are robust, fit a variety of detection function shapes, and have a wide shoulder where detection probability is nearly 1 close to the line transect with a precipitously declining detection probability at some distance from the transect (Buckland 1992). To improve the estimation of the detection probability using these functions, we truncated all data beyond 900 meters for both 2014 and 2016. This facilitated a comparable sampling area between years and across estimation methods. We used Akaike Information Criterion (AIC) to select the most parsimonious model, given available key functions and covariate terms, that best explained detection probability (Burnham and Anderson 2002). We assessed the diagnostic histograms, qq-plots, and the percent coefficient of variation for the most competitive model to ensure our data reasonably fit the model with appropriate precision (Buckland et al. 2004). Once the best model was selected in each year, I estimated abundance, detection probability, and 95% confidence intervals associated with point-estimates.

N-mixture model analysis

As a class of state-space models, N-mixture models explicitly estimate the observation process (the observed state) and the abundance process (the latent ecological state) assuming that animals are detected and counted at spatial units (sites) with imperfect detection. Detection probabilities are site-specific and derived from repeated counts at survey sites. Basic model structure assumes that detections at a site are independent and that all individuals recorded at a given site and time have the same detection probability, although detection can vary by

observation and with covariates (Royle 2004). We used a simple form of the N-mixture model to establish parameter estimation and convergence for our data set, to then be compared to distance sampling estimates using the same data. Because a replicate survey was conducted immediately, we were able to assume population closure and establish parameter estimates for each survey day. However, we were interested in population abundance and detection across survey days in a given year, when deer may have moved into or out of our effective sampling area. To accommodate variation at this time scale, we used an open population modification of the N-mixture model as described by Kery and Schaub (2012), and Dail and Madsen (2011). This approach allowed us to consider each day as a primary occasion when populations could fluctuate and the two replicate observations for each of the spatial units within a day as secondary occasions when populations were assumed closed (Kery and Schaub 2012). Our model used constant parameters for abundance and detection in each sampling period (day). The observation model is shown as:

$$y_{ijk} | N_i \sim Binomial (N_i, p_{i,k}),$$

where y_{ijk} is the total count for each sampling unit i (i = 1...x) during replicate j (j = 1, 2) and day k (k = 1...3). Detections of deer are thus considered binomial random events and are not dependent on individual identification (Royle and Dorazio 2008).

Mean abundance is estimated as the latent state and the count data are assumed to be independent and identically distributed. The basic form of the abundance model is:

$$N_i \sim Poisson(\lambda_i),$$

where *N_i* is the true abundance at sampling location *i*. Although the same observation-level covariates were collected for data used in the N-mixture model, we did not include covariates in this model. We were interested in evaluating a simple form of the observation and process model with count data alone, given the structure of our survey protocol. A Bayesian framework was used to estimate parameters for the N-mixture model using software program JAGS (Plummer et al. 2003) in program R (R team). We assumed vague prior distributions for estimated parameters and evaluated posterior distributions, MCMC mixing plots, and Rhat for model convergence and potential scale reduction factors (Gelman et al. 2006). We used a single, simple form of the abundance and detection model for evaluation so did not rely on model selection as methods for model selection in a Bayesian framework are lacking. Model code is available in Appendix A.

Sensitivity analysis of site size for N mixture models

One challenge posed when using N-mixture models is knowing the effective survey size of a sampled area in continuous habitat for estimation of a species of interest (Kery and Royle 2015). Some studies using the N-mixture model approach have focused on aquatic obligate species that use spatially discrete water bodies, thus avoiding the problem (Zipkin et al. 2014, Lyet et al. 2016). Animal home range size can vary substantially given the behavior and movement of a species, so assumptions must be made for the analysis or a previously estimated home range size used as a boundary reference (Kery and Royle 2015). Distance sampling is exempt from these problems and explicitly addresses the sampling area. This makes simple extrapolations or estimates of animal density difficult to determine from abundance estimates with N-mixture models, specifically. We resolved this issue in two ways. First, we used distance measurements collected during the survey to demarcate an effective strip width for our transect survey. This provided a boundary for distance sampling estimates (a standard truncation width) and for N-

mixture model estimates, where the boundary marked a single side of a rectangular-shaped sampling unit for the latter. The unit side closest to the survey transect was equivalent to the "0" measurement for the distance sampling line transect survey. Then, we selected the total length of the spatial unit along the transect in the north-south direction, completing the sampling unit rectangle. However, as this would have been an arbitrary value based on literature values for deer movement, we developed a sensitivity analysis to evaluate how differing unit lengths (and therefore total spatial unit size) would affect parameter estimates of abundance and detection. We allowed the total number of sites *i* (spatial units) to vary as the length of each site varied, to maintain full coverage of the survey transect area. Given the total length of the survey transect was 21 km, spatial unit length scenarios included 1 km, 2 km, 4 km, 5 km, 6 km, 8 km, and 10 km, allowing a minimum of 2 units along a line transect side and a total of 20 spatial units across the 5 transects. We used spatial coordinates for the start and end points of each survey transect to further constrain the spatial units. Because deer observations were spatially referenced when collected during the aerial survey, observations could be assigned to the appropriate spatial unit, regardless of changing unit length. For each unit size scenario, I ran 1000 N-mixture models with our collected replicated count data and mean parameter estimates.

RESULTS

I collected 172 observations of deer or deer groups in 2014 across 3 surveys, and 341observations across 3 surveys in 2016. Observers flew 5 transects in each survey day for a total transect effort of 125.5 km for each transect, totaling 627.5 km of effort in each year. The encounter rate for deer groups was 0.27 deer/km and 0.54 deer/km in 2014 and 2016, respectively. Conditions were similar across surveys and years, as selected timing and snow cover conditions allowed for clear visibility during all survey days. Observers surveyed deer

within the study area using a fixed-wing aircraft between 24 February and 4 March in both years. Surveys were completed between 1100 and 1400 and generally took 2 hours to complete. All surveys covered a total area of 189 km², which was the transect length (21 km * 5 transects) multiplied by 900 m *2, which was the truncated distance for analysis at 900m on both sides of the transect.

Using distance sampling methods, the most parsimonious model selected by AIC was the half-normal cosine function in 2014 and the hazard rate cosine function in 2016. Given our suite of covariates, the model including observer effects was selected using AIC as the best model for 2014 (Table 2.1). This was not consistent for 2016, when the best model included habitat cover effects rather than observer effects (Table 2.1). Despite differences in covariate inclusion across years, estimates of the probability of detection were essentially the same for both years (p = 0.66; CI: 0.6-0.73 for 2014; p = 0.67; CI: 0.62-0.73 for 2016; Table 2.2). The average abundance estimate across all transects indicated an increase in deer population between years (215; CI: 129-359 for 2014; 425; CI: 277-652 for 2016; Fig. 2.2).

N-mixture models performed well with Rhat values below 1.05 and adequate mixing and convergence of parameters with visual inspection (Gelman and Rubin 1992). We used a spatial unit length of 2 km for all summarized posterior distribution parameter estimates, resulting in 100 spatial units total across the 5 transect area. The mean detection probability as determined from the posterior distribution was higher in 2014 (0.48; CI: 0.443-53) than in 2016 (0.39; CI: 0.35-0.435), although this difference was not substantial (Table 3). Mean deer abundance increased in 2016 from 2014, with approximately twice the deer population estimated in 2016 (699; CI: 630.67 - 787) than in 2014 (311; CI: 277.25 - 356.75, Figure 2.2).



Figure 2.2 A comparison of abundance estimates for white-tailed deer from distance sampling and N-mixture models with associated 95% confidence intervals and 95% credible intervals, respectively. Abundance represents deer within the Maple River study area of Michigan for 2014 and 2016.

The sensitivity analysis using real count data indicated that selected spatial unit size had a significant effect on abundance and detection probability estimates, and their associated variance. Generally, smaller unit sizes that matched home range sizes of white-tailed deer performed well (2 km - 6km), although too small of a unit (1 km) greatly underestimated detection probability and subsequently overestimated abundance in 2014 (Fig. 2.3 and 2.4). Large spatial units consistently provided lower detection probabilities and increased standard deviation in both years (Fig. 2.3-2.6). The 2 km unit size consistently performed the best across years and among unit size scenarios, providing relatively high detection and low deviation, so was chosen for our final parameter estimates (Fig. 2.3-2.6).

Table 2.1 Distance sampling models selected in each year and corresponding data descriptors.

Year	Model; Key function and # adj. terms	k	Tot No observations	Tot. Effort	
			1 ot. 100. Observations	(km)	
2014	Observer; Half-normal, 0	2	172	627.5	
2016	Cover; Hazard rate, 1	3	341	627.5	

Table 2.2 Distance sampling parameter estimates and associated 95% confidence intervals from best fitting models in each year for 2014 and 2016 in Michigan.

				95%CI			95%CI		
Year	Total area (km. ²) of estimation	-	Abundance (N)	lower limit	upper limit	Detection Prob. (P)	lower limit	upper limit	
2014	13	89	215	129	359	0.66	0.6	0.73	
2016	13	89	425	277	652	0.67	0.62	0.73	

Table 2.3 Summarized posterior distributions for N-mixture model parameter estimates, using the 2 km spatial unit, in each year for 2014 and 2016 in Michigan.

Year	Parameter	Mean	SD	2.50%	25%	50%	75%	97.50%	Rhat
2014	Abundance (N)	311.01	20.14	277.25	297	309	323	356.75	1
2014	Detection prob. (p)	0.49	0.02	0.44	0.47	0.48	0.5	0.53	1
2016	Abundance (N)	699.40	39.69	630.67	672	695.67	723.33	787	1
2016	Detection prob. (p)	0.39	0.02	0.349	0.38	0.39	0.41	0.44	1

Credible interval quartiles for each parameter



Figure 2.3 Sensitivity of 2014 N-mixture models to spatial unit size for a) population abundance (N) and b) associated standard deviation (SD) of abundance in Michigan.



Figure 2.4 Sensitivity of 2014 N-mixture models to spatial unit size for a) detection probability (*p*) and b) associated standard deviation (SD) of detection probability.



Figure 2.5 Sensitivity of 2016 N-mixture models to spatial unit size for a) population abundance (N) and b) associated standard deviation (SD) of abundance.



Figure 2.6 Sensitivity of 2014 N-mixture models to spatial unit size for a) detection probability (*p*) and b) associated standard deviation (SD) of detection probability in Michigan

DISCUSSION

We found that application of distance sampling and N-mixture models both produced realistic abundance estimates for white-tailed deer in our study. Distance sampling methods were used according to specifications for aerial application that have been well developed in the literature (Buckland et al. 2001, Fewster and Pople 2008). Aerial survey protocols were easily adjusted for the application of N-mixture models. N-mixture models were effective in estimating abundance and appear to be a practical tool for estimating abundance of a free-ranging wildlife population. Specifically, N-mixture models offered good precision in abundance parameter estimates relative to distance sampling in this case, and met model assumptions. However, we found that estimates from N-mixture models were sensitive to the size of the survey unit selected. While distance sampling has been applied to aerial surveys in the past, to our knowledge, this is the first application of an N-mixture model using an aerial survey for a terrestrial wildlife species. N-mixture models appear to be robust and easily applied to aerial surveys for many species.

Using the distance sampling approach, we estimated detection probability and abundance for deer, providing an independent analysis using a recognized population estimation method. Detection probability estimates were consistently greater than N-mixture model detection probability estimates, although precision was similar to N-mixture models. This parameter may have benefited from the inclusion of covariate data to explain variation in deer observations, although competing models in program DISTANCE with no included covariates had similar detection probability estimates. Abundance estimates were reasonable for our study although they did not demonstrate an increase in population in 2016 as expected.

Distance sampling has been an important tool for wildlife professionals to assess abundance while assessing imperfect detection and has been used with aerial surveys many times over. This is one of the few methods available that explicitly defines the limits of a study area, which is a significant challenge in other estimation methods (Kery and Royle 2015). However, the assumptions of distance sampling may be difficult to meet given environmental or design constraints for some species. For example, if an animal moves in response to a low-flying aircraft and an accurate distance is not recorded at the animal's original location, or if the cover is such that very few detections can be made, reliable estimates cannot be generated. Further, if the aircraft obstructs the transect line, the assumption of perfect detection at the line (distance 0) is violated. This is difficult to address with survey methods, and post-hoc analysis are often used to correct for imperfect detection or surveillance at the transect line. Another important assumption is that animals are statistically independent, are arranged under some stochastic process in the environment, and are distributed independently of a line or point (Buckland et al. 2001). In many landscapes, the distribution of roads, private land, or geophysical barriers make a fully randomized study design difficult, violating this assumption. Finally, aerial surveys often rely on binned distance data from demarcated distance intervals on the aircraft. This presents two challenges, the first being the accuracy of the distance bin assignment for the animal observation at high speeds and varying aircraft yaw. The second occurs in the analytical process when fitting a detection function to the observed distances, as too few bins may result in a poor model fit. Modern field equipment such as range finders may allow improve accuracy, although data should be examined for rounding or heaping issues (where observers record measurements to convenient cut-offs, like 50, 100, 200). If estimating these distance intervals for aerial surveys at a known altitude, each observer must be individually calibrated for sight angle with a clinometer

to ensure standard distances despite observer height. Distance sampling can be accomplished in single or multiple sampling visits with counts and distance measurements, which makes it easy to implement and relatively cost effective, if the above mentioned assumptions are met or easily dealt with (Denes et al. 2015).

The N-mixture model provided reasonable abundance estimates and detection probabilities (Kellner and Swihart 2014). The most significant difference with distance sampling results was in the precision of estimated abundance, with the N-mixture model providing a more precise estimate. We show that N-mixture models were effectively applied to survey a population of deer that increased in abundance over time. This detected population increase was supported by concurrent research from another independent survey in the same study area (Christensen 2017). Population abundance is more often the parameter of interest for wildlife managers and was similar by year for each analytical method. In this case, parameter precision was important as it suggested a significant population increase using the N-mixture model, and no population increase with the distance sampling model. Both modeling approaches tracked an increased mean abundance in 2016, but the interpretation and potential management implications thus varied. The precision afforded by this method allowed a clear interpretation of population change.

We found the abundance and detection parameters estimated with the N-mixture model approach were highly sensitive to the spatial unit size selected in the study design. This addressed an important assumption for N-mixture models. The effective area and shape of a surveyed population in an N-mixture modeling framework is usually not known and subjectively selected by the researcher, revealing a significant source of uncertainty when implementing and interpreting population parameters for any species (Kery and Royle 2015). While some
assumptions can be made about the area in question or the availability of animals within that area in a continuous habitat, we found that directly assessing spatial unit size associated with abundance and detection parameters for deer was critical for our analysis. Ultimately, researchers or managers need to define a population of interest and subsequent survey area the area in some way. It is important to address the spatial extent of a spatial unit for this method, and ideally match these units to ecologically relevant space-use by the animal in study. Evaluation of 7 different spatial unit scenarios indicated that the 2 km spatial selection was ideal. This corresponds closely with a reported value of 140 ha by Hiller et al. (2009) who estimated spaceuse during the winter for white-tailed deer in south-central Michigan. In this regard, distance sampling is explicit and may have an advantage over N-mixture models. Regarding our distance sampling estimates, we were not interested in extrapolating our estimates to a larger study area (which is uncommon for distance sampling), reducing the likelihood of biasing estimates with our selected study design

Aerial surveys are a pillar of wildlife population assessment and have been developed and applied in countless wildlife studies. The advancement of N-mixture models provides an exciting opportunity to improve population estimates using aerial surveys. N-mixture models are less ambiguous when modeling the imperfect detection known to be present in sampling count data and are considered a model-based approach. Detection is not predicated on a single relationship with distance and comes from some common distribution allowing good precision and a clear understanding of relationships with other covariates, if included (Kery et al. 2005). This technique may be a better path forward when faced with uncertainty of fundamental assumptions with traditional methods.

N-mixture models have advantages over traditional distance sampling methods if there is interest in reducing the need for auxiliary data collection (i.e. distance measurements) or other challenges associated with the assumptions required for reliable estimation with distance sampling methods exist. In our case, these models provided a practical field approach and analytical methodology that resulted in precise estimation of unmarked deer. We suggest more applications of these models are needed with field data across taxa and attention must be given to the spatial unit associated with the species' space use. While our current study design required an ad hoc approach to sub-sample collected count data in a manner consistent with N-mixture models, it may provide a good example of application for a species of interest with well-studied population parameters. Recent developments have in fact merged distance sampling and Nmixture binomial modeling approaches as hierarchical distance sampling, which may be including the best of both model classes (Sollmann et al. 2015). These newly developed models use the Dail and Madsen (2011) process model with the standard distance sampling (Buckland et al. 2001) observation model. N-mixture models have been demonstrated to be applicable to zero inflation data and continued to be developed for open and dynamic, stage-structured populations (Dail and Madsen 2011, Zipkin et al. 2014, Denes et al. 2015). This is clearly an area of research interest and current development and application to readily available survey methods, such as aerial surveys, will be important.

APPENDICES

APPENDIX A: R CODE FOR N-MIXTURE MODEL LISTED IN CHAPTER 2

library(R2jags)

library(rjags)

```
load("Aerial2016sims8000m.RData") #load in Rdata sim.dat object
```

dimen <- dim(sim.dat)

```
output <- data.frame(Iteration=integer(),</pre>
```

```
N=numeric(),
sdN=numeric(),
p=numeric(),
sdp=numeric(),
stringsAsFactors=FALSE)
```

```
for (m in 1:dimen[3]){ #dimen[3]){
```

R <-max(sim.dat[,1,m]) #number of sites: read from sim.dat because it will change for different size units

t <-2 #rep. counts (always stays the same)

```
d <-max(sim.dat[,2,m]) #days: read from sim.dat because it will change for different years
```

```
# Create structure to contain counts
```

```
y <- array(dim=c(R,t,d))
for(l in 1:d){
    sel.rows <- sim.dat[,2,m] == 1
    y[,,l] <- sim.dat[sel.rows,3:4,m]
}</pre>
```

```
# Specify model in BUGSlanguage
modelstring = "
model {
    # Priors
    for (k in 1:days) {
        alpha.lam[k] ~dnorm(0,0.01)
```

```
p[k] ~ dunif(0,1)
}
```

Likelihood

Biological model for true abundance
for (k in 1:days) { #loop over d days
lambda[k] <- exp(alpha.lam[k])
for (i in 1:R) { #loop over R sites
N[i,k] ~ dpois(lambda[k]) #abundance</pre>

```
# Observation model for replicated counts
 for (j \text{ in } 1:t){
 y[i,j,k] \sim dbin (p[k], N[i,k]) #detection, looped over 2 secondary reps
  }
  }
  }
 # Derived and other quantities
 for (k in 1:days) {
 totalN[k] <- sum(N[,k]) # Total pop size across all sites
 mean.abundance[k] <- exp(alpha.lam[k])</pre>
  }
 mean.N <- mean(totalN[])</pre>
 mean.p <- mean(p[])</pre>
  }
sink()
tmpf=tempfile()
tmps=file(tmpf,"w")
cat(modelstring,file=tmps)
close(tmps)
```

Bundle data
code for single day
win.data <-list(y=y, R=nrow(y), t=ncol(y), days=d) #y="C" in AHM book</pre>

Initial values
Nst <- apply(y, c(1,3), max) + 1
#Nst[is.na(Nst)] <- 1
inits <-function(){list(N=Nst, alpha.lam = runif(d,-1,1))}</pre>

Parameters monitored
params <-c ("mean.N", "mean.p")</pre>

MCMCsettings ni <-10000 nt <-2 nb <-1000 nc <-3

```
# CallWinBUGSfromR(BRT0.1min)
```

```
#out <-jags(win.data,inits,params,"modelcount2.26.2015.txt",n.chains=nc,
# n.thin =nt,n.iter=ni,n.burnin=nb,debug=TRUE, working.directory=getwd())
#possible using rjags
#model=jags.model(tmpf,data=win.data, inits=inits, n.chains = nc)
#update(model,n.iter=nb) #may be incorrect
#output <- coda.samples(model = model,variable.names = params, n.iter = ni, thin=nt)</pre>
```

```
#jagsout <- as.mcmc.list(out14$BUGSoutput)
#plot(jagsout)
#summary(jagsout)</pre>
```

```
#extract mean and sd for mean.N and mean.p
output[m,1] <- m
output[m,2] <- out16.8test$BUGSoutput$mean$mean.N[1]
output[m,3] <- out16.8test$BUGSoutput$sd$mean.N[1]
output[m,4] <- out16.8test$BUGSoutput$mean$mean.p[1]
output[m,5] <- out16.8test$BUGSoutput$sd$mean.p[1]</pre>
```

```
rm(out16.8test)
print(m)
}
write.csv(output,"output16.8ktest.csv")
```

APPENDIX B: SENSITIVITY ANALYSIS CODE (2KM) FOR CHAPTER 2

```
transect.endpoints <- read.csv("StartPoint.csv")</pre>
```

```
aerial.dat <- read.csv("Aerial2016xy.csv")
```

```
nrep = 1000 #some number of simulations for each unit assignment
```

```
unit.size = 2000 #define unit size (km)
```

n.unit <- floor(21000/unit.size) #calculate number of units of size unit.size that will fit in a transect

len.units <- n.unit * unit.size #total transect dist contained by units

extra.transect <- 21000 - len.units #remaining transect length (not in units)

spacing <- floor(extra.transect/n.unit) #calculate length of breaks between units

#start.point <- floor(runif(1, 0, spacing)) #moved into loop</pre>

unitrows <- n.unit * 2 * 5 #determine total number of units for the study site N,S and 5 transects vdays <- unique(aerial.dat\$Date) #use the data to determine the number of survey days ndays <- length(vdays)

sim.dat <- array(NA, c(unitrows*ndays,4,nrep)) #create an 3D array full of NAs to hold the data for all the iterations

sim.dat[,1,] <- rep(1:unitrows,ndays) #fill the unit numbers in the data array

vector.length <- n.unit * 2 #determine length of vector that will hold break points for units

for (h in 1:nrep){

start.point <- floor(runif(1, 0, spacing))</pre>

for (m in 1:ndays){

#loop through i study areas (we have 2 so I've hard coded that number)

i = 1 #for (i in 1:2){ #maybe unneeded because each year is only one site

#loop through j transects (we have 5 so I've hard coded that number)

for (j in 1:5){

dat <- subset(transect.endpoints, StudyArea==i & Transect==j & Start_Sout==1) #code for study site

ycoord <- dat\$y #read in Y coord for beginning of transect i

breaks <- vector(mode = "integer",vector.length) #create vector to hold start, breaks, and end (full of zeros)

```
breaks[1] <- ycoord + start.point
for (k in seq(2,vector.length-2,2)){
  breaks[k] <- breaks[k-1] + unit.size
  breaks[k+1] <- breaks[k] + spacing
}</pre>
```

```
breaks[vector.length] <- breaks[vector.length-1] + unit.size
```

#fill in data table (unit, day, count1, count2) based on breakpoints

aerial.sub <- subset(aerial.dat, Transect==j)</pre>

north.sub1 <- subset(aerial.sub, Heading_Di == "N" & OBS == 1 & Date == vdays[m]) north.sub2 <- subset(aerial.sub, Heading_Di == "N" & OBS == 2 & Date == vdays[m]) south.sub1 <- subset(aerial.sub, Heading_Di == "S" & OBS == 1 & Date == vdays[m]) south.sub2 <- subset(aerial.sub, Heading_Di == "S" & OBS == 2 & Date == vdays[m])

```
for (l in 1:(n.unit * 2)){
    if (l < (n.unit+1)){
        C1sub <- subset(north.sub2, Y >= breaks[(l*2)-1] & Y <= breaks[l*2])
        C2sub <- subset(south.sub1, Y >= breaks[(l*2)-1] & Y <= breaks[l*2])
    }else{
        C1sub <- subset(south.sub2, Y >= breaks[((l-n.unit)*2)-1] & Y <= breaks[(l-n.unit)*2])
        C2sub <- subset(north.sub1, Y >= breaks[((l-n.unit)*2)-1] & Y <= breaks[(l-n.unit)*2])
    }
    sim.dat[l + (n.unit * 2 * (j-1)) + ((n.unit*2*5) * (m-1)), 3, h] <- sum(C1sub$Group_Size)
        sim.dat[l + (n.unit * 2 * (j-1)) + ((n.unit*2*5) * (m-1)), 4, h] <- sum(C2sub$Group_Size)
        sim.dat[l + (n.unit * 2 * (j-1)) + ((n.unit*2*5) * (m-1)), 2, h] <- vdays[m]
}</pre>
```

}
print(h) #prints iteration to see progress
}
save(sim.dat,file = "Aerial2016sims2000m.RData")
sim.dat[,,2]

LITERATURE CITED

LITERATURE CITED

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CHAPTER 3: THE ROLE OF DROUGHT AS A PREDICTOR OF EMERGENT HEMORRHAGIC DISEASE IN THE EASTERN UNITED STATES.

INTRODUCTION

Vector-borne diseases are responsible for nearly 30% of all emerging infectious disease events in the last decade (Jones et al. 2008). The association between climate change and the ecology of vector populations is important for understanding disease risk as shifting climatic conditions are often associated with increased disease emergence (Guis et al. 2011, Altizer et al. 2013, Paull et al. 2017). Changing climate patterns will affect vector-borne diseases disproportionately more than other disease types, as vector populations and pathogen transmission are sensitive to climatic and environmental factors (Jones et al. 2008, Harvell et al. 2002, Guis et al. 2011). This impact is particularly true in regions where cooler temperatures have traditionally been the limiting threshold for a vector community (Rogers and Randolph 2000). However, the epidemiological dynamics of vector-borne disease are often complicated by other factors, including host dynamics and physical characteristics of the environment, making climatic relationships difficult to evaluate directly (Altizer et al. 2013, Koelle et al. 2005).

Hemorrhagic disease (HD), which includes serogroups in the genus *Orbivirus* for both bluetongue virus (BTV) and epizootic hemorrhagic disease virus (EHDV), is a globally distributed vector-borne disease affecting domestic and wild ruminant species (Nettles and Stallknecht 1992, Mellor and Boorman 1995). The vectors are biting midges in the genus *Culicoides*, which vary in their species distribution, vector competence, and subsequent roles in HD transmission (Gibbs and Greiner 1989, Howerth et al. 2001, Ruder et al. 2015a). In Europe,

significant outbreaks of blue tongue (BT) have caused high mortality in sheep and cattle (> 1 million) as the disease shifted further north and became emergent in the region (Purse et al. 2005). These outbreaks of BT have been linked to climate change and shifting wind patterns affecting *Culicoides* distribution and disease transmission (Wittmann and Baylis 2000, Purse et al. 2005, Wilson and Mellor 2008, Hartemink et al. 2009, Guis et al. 2012). In North America, BT does affect some cattle and sheep annually, but has not resulted in significant domestic animal mortality events, as seen in Europe. Instead, BTV and EHDV serotypes are often the source of acute mortality for wild ruminants, particularly white-tailed deer, although EHDV serotypes are responsible for the majority of clinical sign in these populations (Shope et al. 1960, Ruder et al. 2015a). Because these virus serogroups result in clinically indistinguishable disease in deer, epizootic hemorrhagic disease (EHD) and BT are referred to jointly as HD, which is considered the most significant viral disease for white-tailed deer in North America (Thomas et al. 1974, Nettles and Stallknecht 1992).

Hemorrhagic disease had previously been restricted to the southeastern United States (US) and portions of the Great Plains but recently has expanded north in range and increased in frequency across the Midwest and northeastern US (Stallknecht et al. 2015). The increased frequency and spatial distribution of EHD-related mortality in deer populations at northern latitudes is likely associated with processes affecting vector transmission and host characteristics. Vector transmission and the ecology of BTV- and EHDV-competent *Culicoides* species are sensitive to climatic and environmental conditions, leading researchers to suspect a role of climate and midge habitat on the increase in HD reports for the US (Berry et al. 2013, Ruder et al. 2015a, Ruder et al. 2015b, Stallknecht et al. 2015). The majority of disease in white-tailed deer occurs seasonally when the adult midge transmits the virus after taking a blood meal from

the deer during the summer and early autumn (Mellor et al. 2000). The midge then completes its reproductive cycle and lays eggs in a wet soil substrate, typically near rivers and streams (Wilkening et al. 1985, Purse et al. 2005). Accordingly, wetland features tend to support abundant vector populations in late summer when transmission of the virus to deer occurs (Savini et al. 2011). Further, replication of EHDV serotypes 1, 2, and 7 in a confirmed HD vector (C. sonorensis) has been shown to increase with increasing temperature (Ruder et al. 2015b). Warm temperatures in association with high soil moisture appear to be ideal conditions for both vector and pathogen persistence, although limited data exists on confirmed vector species and transmission rates where HD is emergent (Ruder et al. 2015a). The link between the life-history requirements of the vector and disease occurrence at large scales was supported by correlative research that found long-term (~25 year) increases in wetland cover at a county level helped explain increases in HD morbidity reports across the continental US (Berry et al. 2013). However, wetland features are sensitive to extreme temperatures and changes in precipitation, such as severe drought conditions, suggesting some interaction between wetlands and climatic factors in the vector-host-pathogen dynamic.

Few studies have investigated the role of climate on the spatial and temporal patterns of hemorrhagic disease in the US. Sleeman et al. (2009) found that higher than average winter and summer temperatures, and lower than average spring precipitation, explained annual HD incidence over 5 years in Virginia, where HD is enzootic. In a five-state spatiotemporal analysis, Xu and others (2012) found wind speed, dew point, land surface temperature, rainfall, and NDVI (a measure of vegetative productivity) were important factors explaining HD occurrence in the enzootic Southeast between1980 and 2000. A recent study by Stallknecht and others (2015) found that the number of counties reporting HD had increased between 1980 and 2012 and had

expanded northerly. Further, this study assessed drought severity temporally, using US Drought Monitor (DM) data, which is a widely available indicator of drought intensity incorporating soil moisture and temperature (Svoboda et al. 2002, Stallknecht et al. 2015a). The cumulative DM intensity data for each county and year were positively correlated with years of greater HD reports across the eastern US (Stallknecht et al. 2015). Drought conditions are inherently climate related and commonly considered to occur when environmental conditions are drier than average resulting from warmer than average temperature and lower than average precipitation for some time period. Previous research has alluded to the role of drought on HD but to our knowledge, no study has directly evaluated the spatiotemporal role of drought severity on emerging HD patterns.

The observed heterogeneity of HD mortality reports across the range of the disease and the ability to predict patterns of disease is further complicated by herd immunity dynamics in white-tailed deer (Howerth et al. 2001, Gaydos et al. 2002b). Previous research has indicated that HD meets the criteria for enzootic stability, which occurs when disease-incidence is maximized at moderate levels of disease transmission and seroprevalence within a host population, resulting in high levels of disease infection and low clinical sign (Coleman et al. 2001, Howerth et al. 2001, Stallknecht et al. 1996, Park et al. 2013). The degree of stability refers to the level of infection from a specific pathogen among individuals within a population (Coleman et al. 2001). In the case of HD, acquired and innate immune responses exist and are typically life-long for white-tailed deer (Stallknecht et al. 1991, Gaydos et al. 2002a, Gaydos et al. 2002b). Seroprevalence data and long-term HD datasets have demonstrated endemic stability for HD in the southern regions of the US, with a reduction in seroprevalence and an increase in HD mortality along a north-south latitudinal gradient (Stallknecht et al. 1996, Stallknecht et al.

2015). Using seroprevalence data from 16 states, research by Park and colleagues (2013) found that intermediate levels of infection in a population (~50%) resulted in the greatest number of symptomatic disease cases and mortality reports, which is contrary to commonly predicted positive linear correlations between pathogen transmission and disease incidence (Park et al. 2013). Over time, naïve deer populations will recover as deer are born or immigrate into an affected area, but population recovery and risk for future mortality will be associated with the maintenance of seroprevalence within the population (Park et al. 2013).

Given the vector-borne nature of HD and its increased frequency and intensity in emergent zones, there is a research need to investigate the role of drought as a predictor of HD across the gradient of epidemiological zones of known disease occurrence. Our understanding of the epidemiology of HD is incomplete especially related to identifying risk factors associated with emerging HD outbreaks. I sought to evaluate the role of drought severity on changes in HD reports across the eastern US for a 15-year period when the disease has increased its northern range. My objectives were to 1) develop a spatiotemporal model to evaluate if drought severity and related environmental variables explain changing patterns of HD presence; and 2) to determine if this potential risk factor varies in importance over the present range of HD in the eastern United States. I did this by using spatially-explicit statistical models to evaluate drought severity and related environmental factors (wetland cover and physiographic region) on HD mortality patterns from a longitudinal dataset of presence-absence county-based HD surveillance data. I use remotely sensed data and drought monitor data from a period of known HD reporting increase (2000-2014) to characterize explanatory variables for a spatiotemporal model to address variation in disease patterns over space and time. This approach provides a greatly improved

understanding of the role of drought as a predictor of HD outbreaks across the epidemiological range of the disease.

STUDY AREA

My research focused on counties within 23 states spanning the majority of the eastern US, excluding New England, New York, and Minnesota where HD has not been found prior during the time period of interest. These states included Alabama, Arkansas, Delaware, Florida, Georgia, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maryland, Michigan, Mississippi, Missouri, New Jersey, North Carolina, Ohio, Pennsylvania, South Carolina, Tennessee, Virginia, West Virginia, and Wisconsin. All states had previously reported HD at least once between the years 2000-2014 and represent the epidemiological gradient from enzootic in the southeastern US to emergent and incursive in the upper Midwest and Northeast (Stallknecht et al. 2015). This was demonstrated in the variation of HD occurrence and frequency of reports among the states selected for study (Stallknecht et al. 2015). All states examined in our study were within the known range for white-tailed deer (Hewitt 2011).

METHODS

Data Collection

I acquired data from a longitudinal HD surveillance survey conducted by the Southeastern Cooperative Wildlife Disease Study (SCWDS), at the College of Veterinary Medicine, University of Georgia (Nettles et al. 1992, Stallknecht and Howerth 2004). Surveys have been conducted annually since 1982 for HD status within each county for the entire US by state agency deer biologists and reported to SCWDS. I chose to evaluate 15 years, spanning from 2000-2014, when HD outbreaks precipitously increased in frequency and range across the

eastern US (Stallknecht et al. 2015). Four categories of HD reporting criteria are included in the long-term survey, although I confined the study to the three categories associated with direct deer mortality: 1) sudden and unexplained deer mortality that occurs in late summer and early fall; 2) necropsy diagnosis of HD as determined by a trained professional; and 3) isolation or molecular-based detection of EHDV or BTV. If a county reported any HD mortality in a given year, that county was identified as having HD present (1) in that year, rather than absent (0). Despite existing count data for deer mortalities in many HD reporting counties, I chose a conservative presence-absence approach for disease reporting to reduce uncertainty in reporting bias across states in the annual surveys. In total, 23 states were included, all of which had reported cases of HD within the 15-year time period at the state level. All counties (1,830) within each state were subsequently included in the analysis and all covariate data were estimated at the county level. To account for spatial autocorrelation at the county level, I calculated the spatial centroid for each county using a geographic information system (GIS) and used the resulting latitude and longitude as explanatory covariates (Berry et al. 2013; ArcMap, Environmental Systems Research Institute. Redlands, California, USA).

I calculated drought values for each year and county using the DM tabular data (Svoboda et al. 2002). Archived DM data indicate the percent area of each DM intensity category that is present in a given county, at a given weekly interval throughout the year (http://droughtmonitor.unl.edu/). Drought intensity categories correspond with well-known objective indicators of drought (e.g., Palmer drought severity, standard precipitation, etc.) and include D0, abnormally dry; D1, moderate drought; D2, severe drought; D3, extreme drought, and D4, exceptional drought (Svoboda et al. 2002). These data ranged from 0-100 for any given drought category and year, and were extracted and summed across drought categories for each

county, resulting in a cumulative drought severity and coverage index for each year. The range of cumulative drought severity across all counties and years was 0-500, with a mean of 82.88. The time period selected as the predictive index was the last week in August of each year, as HD reporting for deer is seasonal and peaks during August and September (Howerth et al. 2001, Stallknecht et al. 2015).

Because wetland cover is closely associated with *Culicoides* breeding habitat and reports of HD related deer mortality (Purse et al. 2005, Gaydos et al. 2004, Berry et al. 2013), I created a wetland classification in GIS from the 2006 National Land Cover Database (NLCD) across the 23 state area. I chose 2006 as an index of average available land cover data representing the condition and least potential land cover change for a county within our 2000-2014 year dataset (NLCD data are currently available for 2001, 2006, and 2011 only). I calculated the percentage of wetland within each county based on 30 m pixels of wetland cover, with values ranging from 0% - 93% and a mean of 9%, and included this value as a covariate in the model (Fig. 3.1). I predicted that the amount of wetlands interacts with drought conditions and then affects vector capacity for HD transmission and subsequent HD occurrence. Given this association, I predicted greater percentages of wetland cover would positively correlate with HD occurrence.

Large-scale HD reporting patterns have historically reflected physiographic variation in addition to latitudinal variation (Stallknecht and Howerth 2004, Ruder et al. 2015a). To evaluate the role of this environmental variable on HD presence, I used broad physiographic regions across the 23 state study area including the Appalachian highlands, the Atlantic plain, the interior highlands, the interior plain, and the Laurentian uplands (Fig. 3.2). These regions have broad environmental characteristics that may interact with drought at regional scales and explain HD transmission patterns. I assigned each county a categorical value, based on the physiographic

region that comprised the majority of the area within the county boundaries. No counties in the Laurentian uplands were positive for HD in the study period, so were categorized as the most similar physiographic region.

I predicted that a correlative temporal relationship existed in HD presence by county, dependent on HD presence the previous year. Herd immunity would likely increase in the year following an HD outbreak within a county due to an increase in acquired immunity for deer surviving exposure to BTV or EHDV, potentially reducing HD reporting in subsequent years (Couvillion et al. 1982, Gaydos et al. 2004). However, in a study by Xu and colleagues (2012), a temporal autocorrelation term resulted in the odds of HD occurrence in a county being 0.52 times higher if the county reported HD presence in the previous year. I calculated a temporal autocorrelation term (T), similar to Xu and colleagues (2012) to evaluate the role of a one-year time lag on the probability of HD presence in our study.



Figure 3.1 Wetland cover from 2006 NLCD data across the 1,830 county study area.



Figure 3.2 Physiographic regions of the Eastern US.

Data Analysis

To estimate the role of drought on the probability of HD mortality across the study area, I used a generalized linear mixed model (GLMM) via the "Ime4" package in R 3.4 (R development team 2010). I developed a priori models based on predicted ecological relevance for the spatial and temporal relationship between drought, environment, and HD occurrence, where the response variable was always HD mortality (presence or absence). I fit models with predictors including state and year as random effects, and drought severity, latitude, longitude, physiographic region, and percentage wetland cover as fixed effects. Two random intercepts were allowed to vary by state and year to account for variation among state disease reporting and annual stochasticity respectively. Interaction terms were included between drought and latitude, and drought and wetland (Table 3.1). A temporal autocorrelation term, T_{ij} , was included as a fixed effect to account for HD presence in one year affecting the probability of HD the following year for the same county, where $T_{ij} = Y_{i,j+1}$, with $Y_{i,j+1}$ being the HD response in county *i* if that county had HD present in the previous year. Following a binary GLMM for presenceabsence data, I used a logit-link format to estimate the probability of HD presence (P), in a given county (*i*), and a given year (*j*). The following general model structure was:

$$logit(P_{ij}) = log \frac{(P_{ij})}{1 - P_{ij}} =$$

$$\begin{split} \alpha + \beta_{1} * Drought_{ij} + \beta_{2\dots 5} * Region_{ij} + \beta_{6} Wetland_{i} + \beta_{7} Latitude_{ij} + \beta_{8} Longitude_{ij} \\ + \beta_{9} Drought_{ij} * Latitude_{ij} + \beta_{10} Drought_{ij} * Wetland_{i} + \gamma T_{ij} + Year_{j} \\ + State_{i}, \end{split}$$

where $Year_j \sim N(0, \sigma_a^2)$ and $State_i \sim N(0, \sigma_\delta^2)$.

Model component α is the model intercept, $Drought_{ij}$ is the cumulative drought severity for the last week of August in each year and county, Region_{ii} are categorical variables for the 4 available physiographic regions for each county and year, Wetland is the percent wetland coverage in each county, Latitude is the latitude of each county, Longitude is the longitude of each county, $Drought_{ii} * Latitude_i$ is the interaction between drought and latitude, $Drought_{ii} * Wetland_{ii}$ is the interaction between drought and wetland, *Timelag* is the temporal autocorrelation term, $Year_i$ is the random intercept for year, and $State_i$ is a random effect term for each state. The terms $\beta_{1...k}$ and γ are the fitted parameter coefficients for the predictive variables. I used Akaike's Information Criterion adjusted for small sample size (AICc), to select the most parsimonious model which best explained the probability of HD presence for all preliminary candidate models (Table 3.1, Burnham and Anderson 2002). Univariate models based on the full candidate model were evaluated to assess collinearity and relative variable importance (see Appendix F). All models that were evaluated were conditional on the random effects structure selected initially using AIC. The area under the receiving operating characteristic (ROC) curve was used to assess model fit (Hosmer and Lemeshow 2000).

Table 3.1 Notation, description, and number of parameters providing the base structure for *a priori* models for estimating the probability of HD presence in a county and year during 2000-2014. All models are conditional on the random effects structure selected initially using AIC.

Model notation	Description
$ \begin{array}{l} \alpha + \ \beta_{1} * \ Drought_{ij} + \ \beta_{2\dots 5} * Region_{ij} \\ + \ \beta_{6} Wetland_{i} + \ \beta_{7} Latitude_{i} \\ + \ \beta_{8} Longitude_{ij} \\ + \ \beta_{9} Drought_{ij} * \ Latitude_{ij} \\ + \ \beta_{10} Drought_{ij} * \ Wetland_{ij} \\ + \ \gamma Timelag_{ij} + Year_{j} + Stat \end{array} $	Full model; Drought, physiographic region, % wetland, latitude, longitude, an interaction between drought and latitude, an interaction between drought and wetland, a 1 year time lag effect, a random effect (intercept) for year, and a random effect (intercept) for state te_i
$\begin{aligned} \alpha + \beta_{1} * Drought_{ij} + \beta_{6}Wetland_{i} \\ + \beta_{7}Latitude_{ij} \\ + \beta_{8}Longitude_{ij} \\ + \beta_{9}Drought_{ij} * Latitude_{ij} \\ + \beta_{10}Drought_{ij} * Wetland_{ij} \\ + \gamma Timelag_{ij} + Year_{j} + Stat \end{aligned}$	Drought, % wetland, latitude, longitude, an interaction between drought and latitude, an interaction between drought and wetland, a 1 year time lag effect, a random effect (intercept) for year, and a random effect (intercept) for state te_i
$\begin{aligned} \alpha + \beta_{1} * Drought_{ij} + \beta_{2\dots 5} * Region_{ij} \\ + \beta_{7}Latitude_{ij} \\ + \beta_{8}Longitude_{ij} \\ + \beta_{9}Drought_{ij} * Latitude_{ij} \\ + \gamma Timelag_{ij} + Year_{j} + Stat \end{aligned}$	Drought, physiographic region, latitude, longitude, an interaction between drought and latitude, a 1 year time lag effect, a random effect (intercept) for year, and a random effect (intercept) for state te_i
$\alpha + \beta_1 * Drought_{ij} + \beta_7 Latitude_{ij}$	Drought, latitude, longitude, an interaction between drought and latitude, a l year time log offect, an

+ β₈Longitude_{ij} + β₉Drought_{ij} * Latitude_{ij} + γTimelag_{ij} + Year_j + State_i Drought, latitude, longitude, an interaction between drought and latitude, a 1 year time lag effect, an random effect (intercept) for year, and a random effect (intercept) for state

 $\begin{aligned} \alpha + \ \beta_1 * \ Drought_{ij} + \ \beta_7 Latitude_{ij} \\ + \ \beta_8 Longitude_{ij} + \ \gamma Timelag_{ij} \\ + \ Year_j + State_i \end{aligned}$

Drought, latitude, longitude, a 1 year time lag effect, an random effect (intercept) for year, and a random effect (intercept) for state

RESULTS

I found evidence that drought severity had a significant interaction with large-scale patterns of herd immunity and wetland cover to explain changing patterns of HD presence across 1,830 counties from 2000-2014 (Fig. 3.3, Fig. 3.5). A total of 2,795 counties during the 15 year time period reported presence of HD mortality. The best model using model selection criteria included the full suite of random and fixed effects, except for longitude (See Appendix F). This included 2 interaction terms (drought severity*latitude, drought severity*wetland), the associated fixed effect terms (drought severity, latitude, wetland), categorical fixed effects for physiographic regions and temporal autocorrelation, and random intercepts for state and year, all which contributed to explaining the probability of disease presence in a given year and county (Table 3.2). My statistical model shows clear evidence for the role of drought severity as a predictor for HD presence when modeled as a function of either latitude or wetland cover.

The interaction between drought and latitude proved to be a positive predictor of HD presence in counties that were greater than 33 degrees in latitude. In these counties, as drought severity increased, the probability of HD increased (Fig. 3.3). The magnitude of predictive strength increased significantly with increasing latitude, with a probability of HD presence reaching nearly 0.40 in the most severe drought conditions at 45 degrees latitude (counties in the states of Michigan and Wisconsin, Fig. 3.3, Fig. 3.4). Alternatively, drought severity was not predictive in southern latitudes (latitudes of 30-35 degrees), with a probability of HD presence consistently near 0.15 across drought conditions. High levels of population-level HD seroprevalence have been demonstrated for this region and fewer susceptible animals are likely (Howerth et al. 2001, Stallknecht et al. 1996, Park et al. 2013, Stallknecht et al. 2015). Further, drought was an important predictor when interacted with wetland in the model. The total percent

of wetland cover for each county interacted with drought severity across the study area, reducing the probability of HD with increasing wetland values. So, as wetland cover and drought severity increased, the probability of HD presence decreased. However, the effect of this relationship was minimal, becoming less significant with increasing percent wetland.

The physiographic region for each county was an important predictor in the best model as a categorical variable, although the significance varied across the four regions. The Appalachian Highlands was the intercept reference category and had a positive relationship with the probability of HD presence. The odds of HD presence in the Interior Highlands was slightly greater than the Appalachian highlands (9%), while the odds of HD presence in the Atlantic plains or the Interior plains was lower than the Application highlands (37% and 12%, respectively, Table 3.3).

Both random effects were included in all models based on AIC. For the best model, the random effect average State variance was 0.82 (SD = 0.91) and the average Year variance was 0.81 (SD = 0.90). I included both latitude and longitude centroids for each county in my predictive model to incorporate spatial covariates which would address my prediction of spatial autocorrelation of HD presence among neighboring counties (Barry et al. 2013). However, the longitude term was not a significant variable in any model and there was little ecological justification for including this term. Thus, despite the global model having a competitive Δ AICc value (within 2 units), I chose not to include this model in my final estimates as it was not more informative and likely an over parameterization to improve model fit. Alternatively, latitude had strong justification for inclusion as a spatially explicit predictive term and as an ecological prediction. Latitude was a surrogate term for herd immunity in this model, given previous evidence for endemic stability in southern states within the US (Stallkencht et al. 1996, Park et

al. 2013, Stallknecht et al. 2015). The interaction between drought severity and latitude, as mentioned earlier, greatly varied as a risk factor for HD presence in a north-south gradient across the eastern US. This tells us that the coefficient of drought severity depends on the value of latitude and vice versa.

Finally, I found the temporal autocorrelation term was a strong positive predictor of HD presence in a given county and year, similar to previous research using a similar temporal covariate (Xu et al. 2012). If a given county had HD present in a given year, the following year was twice as likely to have HD present in that county (Table 3.2). For the best model, I used the area under the ROC curve to evaluate the sensitivity and specificity of the model and found the best model had acceptable discrimination with a value of 0.726 (See Appendix D, Hosmer and Lemeshow 2000).



Figure 3.3 The probability of HD mortality presence with associated standard error (shaded area) in logit scale on the y-axis and cumulative drought severity on the x-axis. The relationships are then grouped by latitude. As latitude increases the slope of the line increases.



Figure 3.4 The change in the marginal effect of latitude on the coefficient of drought severity with associated standard error (shaded area). This demonstrates the statistical significance of these conditional coefficients and the relationship between the interacting model terms (drought severity and latitude). With increasing latitude the magnitude increases for the coefficient of drought severity on HD mortality. A superimposed histogram is included at the bottom of the marginal effect plot to view the distribution of the data.



Figure 3.5 The probability of HD mortality presence with associated standard error (shaded area) in logit scale given the percent wetland cover by county and the interaction with drought severity

Fixed effects:	Estimate	Std. Error	z value	Pr(> z)	Significance	Odds Ratio
(Intercept)Region1	3.350	0.969	3.458	0.001	***	28.503
Drought Severity	-0.016	0.001	-21.478	< 2e-16	***	0.984
Latitude	-0.167	0.024	-6.835	0.000	***	0.846
Wetland	0.106	0.043	2.482	0.013	*	1.112
Region2	-0.455	0.102	-4.464	0.000	***	0.635
Region3	0.085	0.145	0.589	0.556		1.089
Region4	-0.126	0.106	-1.191	0.234		0.881
TAuto	0.698	0.072	9.748	< 2e-16	***	2.010
Drought: Latitude	0.001	0.000	25.728	< 2e-16	***	1.001
Drought: Wetland	-0.001	0.000	-3.765	0.000	***	0.999

Table 3.2 Average coefficient estimates for the fixed effect parameters for HD mortality presence by county across 23 states in the eastern US, for 2000-2014.

DISCUSSION

I found that extreme drought, when interacting with latitude, is a strong predictor of the occurrence of HD outbreaks in regions with emerging and incursive epizootic HD events. The influence of a single climatic predictor, drought severity, has never been assessed at a large spatial-temporal scale for HD outbreaks. Interestingly, this climatic force was most informative when allowed to vary across a latitudinal gradient and with varying wetland cover at the county level. Further, models were significantly improved when HD presence in a previous year was accounted for, proving the importance of temporal effects between years. My research provides spatially explicit evidence for the link between climate forces and emerging disease patterns across the range of this disease using a widely available drought severity index.

I demonstrated the role of a specific climate variable, drought severity, as a predictor of HD occurrence across the eastern US. My resulting spatio-temporal model confirmed the importance of the interaction of drought severity with environmental characteristics to explain changing patterns of HD presence. The interaction between drought and wetland cover, in

particular, was indicative of the vector ecology associated with HD. Culicoides species have specific breeding habitat requirements which are typically associated with soils bordering wetland systems and riparian habitats (Wilkening et al. 1985). Because these water-oriented systems are inherently affected by changing water dynamics and drought conditions, the interaction of drought and wetland in the model was important for understanding one aspect of vector-driven spatial heterogeneity across our study. Increased wetland area in a county was initially believed to equate to an increased potential for midge population abundance in late summer. While I did not have information to inform this mechanistic relationship, I did find that the predictive effect of increased percent wetland cover at a county scale varied with increased drought severity (Fig. 3.5). At low levels of wetland cover, the relationship with drought was slightly positive, increasing the probability of HD with increased drought severity (Fig. 3.5). However, when wetland cover was within the top 20%, the relationship between wetlands and drought shifted to that of a protective effect, where increased wetland cover reduced the probability of HD presence (Fig. 3.5). This relationship may be explained by counties that are primarily wetland cover having less available high-quality habitat for deer, and thus reducing the overall likelihood of the vector interacting with the host. Alternatively, extremely high wetland cover in an area may not be ideal habitat for midge species responsible for HD transmission.

The forces driving recent changes in HD patterns have not been well studied, particularly for emergent regions of disease where mortality of white-tailed deer is most severe. This is due, in part, to the complex epidemiology of HD. The transmission of this disease varies spatially in a north-south gradient, mirroring a pattern of endemic stability across the known range of the disease (Stallknecht et al. 1996, Park et al. 2013, Stallknecht et al. 2015). Endemic stability has been demonstrated for HD, and results in heterogeneous disease transmission and herd immunity
across large spatial scales (Park et al. 2013, Howerth et al. 2001). Accordingly, in the most southern counties in the study where HD is enzootic, drought severity was not an important predictor of disease, lending to the theory of herd immunity as a driving epidemiological force in endemic regions (Park et al. 2013). With precipitous increases in latitude, however, I demonstrated the increasing strength of drought severity as a predictor of disease presence (Fig. 3.3, Fig. 3.4). Thus, I addressed my initial objective to determine the importance of variation in drought severity as a risk factor over the present range of HD in the eastern United States. My finding was similar to a recent study of West Nile virus (WNV) patterns in humans, where the primary forces explaining interannual variation for this disease included drought and immunity, where regions with low immunity were predicted to have the greatest WNV epidemics (Paull et al. 2017). Vector-borne diseases are susceptible to climate variation and, given these findings, one can assume that if extreme drought severity increases, increase in HD occurrence in epizootic and incursive regions may increase.

Temporal autocorrelation was predictive of HD presence in white-tailed deer for a given county and year, but with a different relationship to previous-year HD outbreaks than expected. I predicted that if HD was present in a county in one year, the following year would have a negative correlation in HD presence due to fewer susceptible deer being available for infection, and thus mortality reporting. Rather, I found a positive relationship with previous-year HD status, with the odds of disease reporting to be twice as likely if HD was reported the year before in the same county (Table 3.2). While this relationship was initially counterintuitive, the transmission and accumulation of herd immunity for white-tailed deer is locally patchy and may not be homogenous within a county (Ruder et al. 2015a). Further, the relationship with increased HD seroprevalence for a population is non-linear with respect to HD reporting (Park et al. 2013),

which challenges the assumption that increased HD reporting always results in increased herd immunity. Regardless, the correlation between adjacent reporting years was an important predictor of HD presence over the 15-year study period.

Vector-borne diseases are considered to be most at risk of increasing their distribution and frequency with predicted climate change scenarios (Harvell et al. 2002). The population ecology and distribution of *Culicoides* species plays a significant role in the epidemiology of hemorrhagic diseases (Mellor et al. 2000, Wilson and Mellor 2008, Savini et al. 2011). Midges, in particular, have recently expanded their range northward in many regions, which has been largely attributed to milder winter temperatures (Harvell et al. 2002). Due to the vector-borne nature of HD, the prevalence of the disease is frequency-dependent and influenced by climatic variables (Gaydos et al. 2004, Sleeman et al. 2009, Xu et al. 2012, Ruder et al. 2015). In North America, adult-stage midges associated with HD die shortly after the first frost in autumn (Nettles and Stallknecht 1992). If predictions of warmer average temperature are correct, the basic reproduction number (R0) of pathogens is expected to increase and the pathogen will persist longer on the landscape (Harvell et al. 2002). This spatial-temporal drought severity model will provide insight for predicting areas at risk for future disease outbreaks.

MANAGEMENT IMPLICATIONS

My research was intended to better understand the drivers of HD across a large spatialtemporal gradient experiencing high variation in HD mortality events. Outbreaks of HD often result in a devastating impact on local deer populations in epizootic and incursive disease regions (Fischer et al. 1995, Gaydos et al. 2004, Stevens et al. 2015). However, managing these local mortality events is extremely difficult due to multiple factors affecting the high annual variation of the disease. Host dynamics can be complex and affect disease transmission dynamics. Based

on this study, the way in which drought severity and herd immunity interact may have important consequences for local and regional management of deer populations.

The population impacts of increasing HD mortality and the subsequent management implications are complicated by herd immunity dynamics, which is demonstrated by variation of HD presence across latitude in the study. Given the apparent high mortality rates for naïve deer populations, HD can be considered to have top-down effects on deer abundance, producing direct numeric reductions in the population (Gaydos et al. 2004, Holdo et al. 2009). Recent work by Park et al. (2013) demonstrated that across a 16 state region, a greater probability of reporting deer with HD symptoms occurred when deer population seroprevalence was intermediate (around 50%). However, this study did not include recent disease reports in the upper Midwest or Northeastern US where severe clinical disease and mortality have been observed (Stallknecht et al. 2015). Typically, a disease outbreak that occurs within the lifespan of an animal will result in antibody development or death upon infection, leaving a percentage of the population with immunity to the pathogen. If a local deer population is not able to accumulate sufficient immunity from pathogen exposure among individuals, deer populations may be prone to continued die-offs given optimal environmental conditions (including severe drought) for disease transmission. The effects of disease on the population dynamics of wildlife species depend on the epidemiological zone the population is within and the associated epizootiology for the given species (Gulland 1995, Osnas et al. 2009, Ruder et al. 2015). Epizootic disease events may result in mass mortalities of animals which, coupled with stochastic events, can lead to extirpation of local populations or species extinction (Harwood and Hall 1990). White-tailed deer are a highly valued native wildlife species across the US and may be at risk of increased disease events in regions of emergent HD.

Unfortunately, HD will remain difficult to manage in free-ranging deer populations. HD mortality is not likely to increase with greater deer density and is not assumed to be sex- or ageclass specific (Fischer et al. 1995, Begon et al. 2002). However, maternal antibodies are transmitted to fawns and persist for up to 18 weeks, resulting in protection of young deer from late summer EHD outbreaks, regardless of drought conditions (Gaydos et al. 2002c). Over time, deer populations will recolonize as reproduction continues and new deer immigrate into an area, but this may be influenced by social structuring and movement rates (Porter et al. 1991). Midge control options may be viable for isolated, localized wetlands, but is not a practical management option at larger scales. Further, the relationship between wetlands and HD transmission appears to vary at differing spatial scales, indicating more research is needed to understand the ecological relationship between the disease vector and wetland dynamics.

HD is an emerging and reemerging issue globally. Similar to increasing HD presence in northern US states, several other countries have observed increases in morbidity and mortality of domestic ungulates infected with bluetongue virus. Emergent bluetongue outbreaks in Europe, Northern Africa, and the Middle East have resulted in large mortality events and economic losses. Researchers have found that wind dispersal and warmer temperatures have resulted in the successful invasion of new vector species and subsequent disease occurrence (Purse et al. 2005). While North America has not suffered the same type of loses from bluetongue virus in domestic animals, there is concern that newly emergent HD serotypes may result in increased mortality for both wild and domestic animals in the future. Continued efforts to understand the role of climate on vector-borne disease patterns will be of increasing importance as climate change occurs and diseases continue to spread in to naïve populations.

APPENDICES

APPENDIX A: MODEL VALIDATION RESULTS FOR CHAPTER 3

Area under the ROC curve for best model: 0.7252321

Associated R code for AUC value: auc(roc(prob2,as.factor(FULLFE2\$model\$HDMORT)))

APPENDIX B: MODEL OUTPUT FOR BEST MODEL FOR CHAPTER 3

HD32 output Generalized linear mixed model fit by maximum likelihood (Laplace Approximation) ['glmerMod'] Family: binomial (logit) Formula: HDMORT ~ SUM * CENTROID_Y.y + SUM * Wetland + SUM + CENTROID Y.y + Wetland + physio + (1 | fYear) + (1 | fState.y) + TAutoData: Alldatacombo AIC BIC logLik deviance df.resid 13128.7 13226.5 -6552.4 13104.7 25608 Scaled residuals: 1Q Median Min 3Q Max -2.3936 -0.2974 -0.1912 -0.1277 14.7954 Random effects: Groups Name Variance Std.Dev. fState.y (Intercept) 0.8141 0.9023 fYear (Intercept) 0.8059 0.8977 Number of obs: 25620, groups: fState.y, 23; fYear, 14 Fixed effects: Estimate Std. Error z value Pr(>|z|)*** 3.35E+00 9.69E-01 3.458 0.000543 (Intercept) *** 7.46E-04 SUM -1.60E-02 -21.478 < 2e-16 CENTROID_Y.y *** -1.67E-01 2.44E-02 -6.835 8.22E-12 Wetland 1.06E-01 4.28E-02 2.482 0.013083 * *** physio2 -4.55E-01 1.02E-01 -4.464 8.04E-06 physio3 8.55E-02 1.45E-01 0.589 0.555867 physio4 -1.26E-01 1.06E-01 -1.191 0.233563 *** TAuto 6.98E-01 7.16E-02 9.748 < 2e-16 SUM:CENTROID Y.y 5.220e-04 2.03E-05 25.728 < 2e-16 *** SUM:Wetland -8.67E-04 2.30E-04 -3.765 0.000166 *** 01 '**' 0.0 Signif. codes: 0 '***' 0.0 1 '*' 0.05 '.' 0. 1 ' ' 1 Correlation of Fixed Effects: (Intr) SUM CENTRO Wetlnd physi2 physi3 physi4 TAuto SUM:CE SUM -0.064 CENTROID_Y. -0.946 0.066

Wetland -0.097 0.076 0.120

physio2-0.277-0.0070.245-0.403physio3-0.1750.0110.144-0.1130.394physio40.0920.011-0.148-0.1700.3160.540

TAuto -0.050 -0.004 0.039 -0.007 0.037 0.010 0.001

SUM:CENTROID 0.078 -0.967 -0.085 -0.080 -0.007 -0.009 -0.012 0.010

SUM:Wetland 0.147 -0.028 -0.152 -0.321 -0.199 -0.075 -0.014 0.001 0.097

APPENDIX C: SUPPLEMENTARY MODEL SELECTION DATA FOR CHAPTER 2

Table C.1 Full model selection table using AIC criteria for all model variations predicting the probability of HD presence in 1830 counties within 23 states during 2000-2014.

Model Name	Κ	AICc	Delta_AICc	AICcWt	Cum.Wt	LL
Drought*Latitude, Drought*Wetland +	12	13129.7	0	0.71	0.71	-6552.84
Physio + T						
Global Model	13	13131.55	1.85	0.28	0.99	-6552.77
Drought*Latitude, + physio +T	10	13139.51	9.81	0.01	0.99	-6559.75
Drought*Latitude, + wetland + Physio +T	11	13140.24	10.54	0	1	-6559.11
Drought*Latitude + Wetland + Physio +	12	13141.93	12.23	0	1	-6558.96
long +T						
Drought*Latitude, Drought *Wetland +T	9	13149.38	19.68	0	1	-6565.68
Drought*Latitude, + Wetland + T	8	13168.23	38.53	0	1	-6576.11
Drought*Latitude, + Long +T	8	13174.34	44.64	0	1	-6579.17
Drought *Wetland + Latitude + Long +	12	13216.18	86.48	0	1	-6596.09
Physio +T						
Drought *Wetland +T	8	13233.75	104.05	0	1	-6608.87
Drought + Latitude + physio + Wetland	10	13254.65	124.95	0	1	-6617.32
+T						
Drought + Latitude + Long + Wetland +	11	13256.43	126.73	0	1	-6617.21
Physio +T						
Drought + Physio + Latitude +T	9	13260.06	130.36	0	1	-6621.03
Drought + Latitude + Long + physio + T	10	13260.92	131.22	0	1	-6620.46
Drought + Latitude + T	6	13291.16	161.46	0	1	-6639.58
Drought + Latitude + Wetland + T	7	13292.08	162.38	0	1	-6639.04
Drought + Physio	8	13293.72	164.02	0	1	-6638.86
Drought + Latitude + Long + Wetland	8	13293.98	164.28	0	1	-6638.99
Drought + Long + T	6	13316.88	187.18	0	1	-6652.44
Drought + Wetland	6	13316.99	187.29	0	1	-6652.5
wetland + physio	8	13662.93	533.23	0	1	-6823.46
Latitude + T	5	13664.22	534.52	0	1	-6827.11
Temporal autocorrelation (T)	4	13686.02	556.32	0	1	-6839.01
Drought Latitude interaction	6	13839.47	709.77	0	1	-6913.73
Drought Physio Inter	10	13848.59	718.89	0	1	-6914.29

Table C.1 (cont'd)

Drought Wetland Inter + Latitude	7	13896.97	767.27	0	1	-6941.48
Drought Wetland Interaction	6	13918.24	788.54	0	1	-6953.12
Latitude + Drought Categories	9	13959.1	829.4	0	1	-6970.55
Longitude Drought interaction	6	13977.4	847.7	0	1	-6982.7
Drought categories	8	13980.75	851.05	0	1	-6982.37
Drought	4	13998.9	869.2	0	1	-6995.45
Physio	6	14345.75	1216.05	0	1	-7166.87
Latitude + Wetland + T	5	14354.81	1225.11	0	1	-7172.4
Latitude	4	14368.94	1239.24	0	1	-7180.47
Wetland	4	14382.19	1252.49	0	1	-7187.09
Longitude	4	14386.59	1256.89	0	1	-7189.3
Intercepts only null model	3	14388.51	1258.81	0	1	-7191.26

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POSTFACE

By investigating the local distribution and population-level impacts on deer in areas affected by EHD, developing and applying population estimation techniques appropriate for localized population change assessment, and evaluating landscape-level drivers of hemorrhagic disease across an epidemiological gradient, I was able to address uncertainties on the population impacts and risks of emergent EHD for white-tailed deer. I briefly review my findings in this section and discuss relevant research needs for future study.

Chapter 1 sought to determine whether localized deer population impacts occurred after a severe EHD outbreak in 2012 in Michigan. The experimental study design implemented allowed me to relate population impacts to EHD and demonstrate the local spatial distribution of population impacts relative to a high-risk riparian habitat. Analyses confirmed that population impacts did occur and were attributable to EHD mortality. These impacts were most severe within 1 km of a river corridor with known EHD reports and dissipated within 5 km of an EHD focal area. These findings were substantiated by comparison to a non-disease site within Michigan, where deer populations were stable across habitat types and over time. Further, where population impacts were observed, we consistently detected annual population increases over the 4-year monitoring period following the disease outbreak. This increase over time provided evidence of deer population recovery after a sudden and localized population depression.

Chapter 2 sought to develop and apply population estimation methods for localized assessment of deer populations. This was accomplished using aerial surveys and implementing both distance sampling (Buckland et al. 2001) and N-mixture models (Royle 2004) for count data collected from line-transects. Further, N-mixture models were evaluated for sensitivity to

spatial unit size selection. Analyses of this chapter demonstrated similar population estimates beween analytical frameworks, indicating that N-mixture models were successfully applied to aerial survey data for deer. Increased precision of abundance estimates for the N-mixture models compared to distance sampling estimates resulted in the clear demonstration of a population increase over time (abundance was greater in 2016 than 2014). These results mirror findings from ground surveys conducted annually for the same study area during summer months. Population impacts from EHD mortality in 2012 were suspected in this area and population increases align with these predictions. Finally, we found that abundance and detection probability estimates for N-mixture models was highly sensitive to the selection of spatial unit size. Spatial units most similar to the movement ecology of deer (2000 m x 900 m) provided realistic values and acceptable variance for abundance and detection parameters.

Chapter 3 sought to evaluate the role of large-scale drought severity across the epidemiological range of hemorrhagic disease (HD) in the eastern United States. A 15-year data set of HD occurrence by county from an annual survey conducted by the Southeastern cooperative wildlife disease study was analyzed in this chapter. I developed a spatial temporal model to evaluate drought severity and related environmental variables that might explain changing patterns of hemorrhagic disease presence. My results indicated that drought severity had a significant interaction with herd immunity, modeled as on index of latitude. As latitude increased into northern regions were HD outbreaks are epidemic or incursive, the predictive value for drought severity on HD presence increased significantly. This relationship was not important in the southeastern US, where high seroprevelence and frequent HD events occur. Further, the presence of HD was positively related to whether disease had occurred in the county in the previous year and if the county existed in the Interior Highlands physiographic region.

These findings provide clear evidence of climate-based drivers of HD across the range of the disease.

Areas of future research to inform EHD epidemiology and wildlife impacts should include proactive herd immunity surveillance, regional vector confirmation, and refined largescale modeling efforts. These areas of focus will fill gaps in our understanding of the epidemiology of the disease and improve our ability to predict future mortality events. Systematic seroprevalence information for Michigan and other states experiencing epidemic EHD outbreaks should be collected to create a clear spatial distribution of enzootic, epidemic, and incursive regions of the disease. Seroprevalence within a deer population will inform the proportion of susceptible individuals within the population and subsequently the risk associated with future HD outbreaks. Culicoides surveys using standard protocols should be conducted in conjunction with outbreaks to help determine regionally specific vectors and life-stage requirements. Continued landscape-level modeling efforts of characteristics affecting midge presence and disease occurrence, and forecasting models predicting EHD outbreaks under varying immunity, climate, and land use scenarios would be informative for understanding current and future conditions conducive to HD presence. Finally, state agencies should develop systematic and consistent surveillance plans for assessing outbreak impacts of EHD. If deer mortality information were collected using similar methods and survey designs across regions, outbreak impacts could be mapped and compared for disease management and epidemiological characterization.

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