

FACTORS AFFECTING CHRONIC WASTING DISEASE PRION TRANSMISSION AMONG
WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) IN SOUTHERN MICHIGAN

By

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ABSTRACT

The potential for direct and indirect transmission of Chronic Wasting Disease (CWD)-causing prions increases as deer gather, and understanding factors affecting deer space use and grouping behavior can help managers identify areas where deer may congregate in winter. Additionally, deer interactions and behaviors play an important role in direct transmission of prions. My objectives in this study were to identify environmental and landscape features that influence deer group size, and quantify behaviors exhibited by deer at congregation areas including baited sites, food plots, and naturally occurring forage. I used road-based and camera-trapping surveys from January-April 2021 and 2022, throughout a 4,262 km² area in southern Michigan. On road surveys, I observed 603 deer groups and group sizes ranged from 1 – 67 deer. From trail camera footage, I conducted over 2,000 direct behavioral observations (bait sites = 1,631, food plots = 416). My results indicate that potential areas for larger deer group sizes include larger corn and forage crop fields adjacent to woodlots that are >220m away from buildings. For all deer observed, I detected significantly fewer direct contacts at food plots ($\beta_{\text{Food plot}} = -1.45$ [95% CI = -2.00 - -0.90]) and transects ($\beta_{\text{Transects}} = -1.12$ [95% CI = -1.64 – 0.59]) compared to bait sites. I observed fewer environmental contacts at food plots ($\beta_{\text{Food plot}} = -0.68$ (95% CI = -0.90 - -0.47) and transects ($\beta_{\text{Transects}} = -0.65$ (95% CI = -0.87 - -0.43) compared to bait sites. Additionally, direct contacts varied by deer sex and age class at bait sites, including adult males had an increased likelihood of contacts as the number of male fawns present increased ($\beta_{\text{Male fawns}} = 0.45$ [95% CI = 0.19 – 0.71]). My results indicate that in areas of CWD concern, food plots and naturally occurring forage offer a less risky food source for deer. This information can inform simulation models designed to assess CWD transmission.

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INTRODUCTION

Chronic wasting disease (CWD) belongs to a family of pathogens called transmissible spongiform encephalopathies (Williams 2005). It is a unique, neurodegenerative pathogen that is contagious and always fatal among cervids once contracted (Williams 2005). Prions, a type of protein found in the brain that induces abnormal folding in other neural proteins, causes CWD (Williams 2005). This abnormal folding results in spongiform changes in brain tissue, leading to signs of disease: emaciation, drooling and excessive thirst, lack of coordination, loss of awareness, and decreased fear of humans in cervids (Williams and Young 1980). Chronic wasting disease is known to have a long incubation period, taking approximately 16 months before clinical signs are exhibited (Henderson et al. 2015). Individuals may begin shedding infectious prions as early as 3 months post-infection (Henderson et al. 2015). The long incubation period coupled with rapid decline in health following the first noticeable signs of CWD make it extremely difficult to identify infected cervids. Chronic wasting disease was first documented at a research facility in Colorado during the 1960's, since then it has expanded nationally and globally (Williams and Miller 2002). During the late 1970's in Wyoming, CWD was identified in captive mule deer (*Odocoileus hemionus*; Williams and Young 1980). Infected deer and elk (*Cervus canadensis*) were subsequently found in zoological parks in the US and Canada (Williams and Young 1992). In 1981, CWD was documented in a free-ranging elk in Colorado, spurring surveillance that resulted in additional positive detections in free-ranging elk in Wyoming, and free-ranging mule deer and white-tailed deer (*Odocoileus virginianus*) in Colorado and Wyoming (Williams and Miller 2002). Spread potentially occurred through interactions between captive and free-ranging individuals and interchanging of infected individuals between captive facilities (Williams et al. 2002; Osterholm et al. 2019). However, it

remains unknown whether CWD first arose in captive or free-ranging populations. Since the 1980's, CWD has continued to expand nationally and globally. Positive cases have been documented in 5 other countries including Canada, Finland, Norway, South Korea, and Sweden (United States Geological Service 2023). Three Canadian provinces and South Korea first identified CWD when an infected cervid was imported into a game farm (Osterholm et al. 2019). Within the United States, twelve states, including Michigan, first detected CWD in captive deer (Thompson et al. 2023).

In 2008, CWD was first documented in a captive cervid facility in the southwest Lower Peninsula of Michigan. In 2015, CWD was documented in a free-ranging white-tailed deer in the south-central Lower Peninsula. Surveillance of the surrounding area started, and 2 years later a CWD outbreak was identified in the area where the captive animal was detected (CWDA 2015). Since the initial case in a free-ranging deer, CWD has expanded in Michigan. Deer that tested positive for CWD have been detected in the Lower and Upper Peninsulas (MDNRa 2023). Within Michigan, CWD has been found in both suburban and rural areas. One of the many challenges facing managers is trying to understand the factors having the greatest influence on CWD transmission and if active management can slow spread.

Prions are difficult to inactivate, persisting in the environment for a decade or more (Smith et al. 2011), and are highly contagious (Mathiason et al. 2009). Several methods for prion inactivation include autoclaving at 134 °C, alkaline detergents (Sakudo 2020), bleach solution (Williams et al. 2019), and peroxymonosulfate solution (Chesney et al. 2016). Deer will shed prions through mucous, blood, saliva, feces, and urine (Miller et al. 2004; Mathiason et al. 2006; Haley et al. 2016). Prions may be transmitted through direct physical contact (Schauber et al. 2015; Mejía-Salazar et al. 2017) or contact of deer with elements of their environment, such as

contaminated soil or food sources (Miller et al. 2004). In one study, 3 of 12 penned deer were indirectly infected with CWD when exposed to areas where infected, decomposing deer carcasses were deposited, despite not coming into direct contact with carcasses (Miller et al. 2004). Two years post-decontamination, penned deer still developed clinical signs of CWD after being introduced to a formerly infected area (Mathiason et al. 2009). As deer shed prions through bodily fluids or tissues in localized areas (e.g., infected deer home range), the environment becomes increasingly contaminated with infectious prions. Prions bind to soil and remain stagnant in the soil column, allowing them to persist in soil for years (Smith et al. 2011). Hence, naïve deer can be exposed to prions directly through animal-to-animal contact, or indirectly through the environment. If the naïve deer is susceptible to infection, the exposed individual becomes infected resulting in disease. A considerable knowledge gap exists in quantifying pathways of CWD transmission (Mysterud and Edmunds 2019), and information on direct and environmental deer contacts perceived to increase likelihood of CWD transmission is lacking (Miller et al. 2004; Potapov et al. 2013; Mejía-Salazar et al. 2017).

Sparse literature exists that defines and describes the multitude of behaviors that deer exhibit. Of the limited studies available, many focus on aggressive behaviors displayed in various settings and interaction rates between different sex and age classes (Ozoga 1972; Hirth 1977; Garner 2001). Research depicting non-aggressive forms of behavior is almost non-existent. In Georgia, a study categorized threats, displacements, and strikes as aggressive deer behaviors, with the only non-aggressive behaviors identified as grooming and suckling (Lagory 1986). Hirth (1977) described aggressive deer behaviors in the form of threats, chasing, and ear-drop among various sex and age classes; 36 observations of grooming behavior and 18 nose-touch behavior events were observed. In a northern Michigan winter deer yard with 77

deer/km², Ozoga (1972) recorded pushing, rushing, striking, and flailing behaviors in addition to several of the other aggressive behaviors previously mentioned. Interactions can vary among sex and age classes of deer, and among related and unrelated individuals. Interaction rates between adult females, and between adult females and yearlings is low, with most interactions being aggressive because of intolerance towards each other (Hirth 1977). Most interactions of females will occur between relatives, and there is low tolerance of non-relatives (Nixon et al. 1991). Adult males maintain bachelor groups post-breeding season, therefore interacting with other adult or yearling males throughout most of the year (Nixon et al. 1994).

Until now, direct physical contact rates among deer have generally been assumed based on telemetry collar proximity data for deer located ≤ 25 m apart (Kjaer et al. 2008; Williams 2010; Tosa et al. 2016). Deer are more likely to make direct physical contact with members of their own social group rather than members outside of their group (Schauber et al. 2007). Adult female to adult female interactions were more common than adult female to yearling female and varied depending on time of year in one study (Hirth 1977). Interaction rates between males is also low during the non-breeding season and most behaviors are aggressive, consisting of posturing and chasing (Hirth 1977). Direct physical contact within groups greatly increases pathogen transmission within a small area (Garner 2001; Cosgrove et al. 2018), but little is understood about how between-group contact causes CWD to spread throughout a population. It is unknown if landscape characteristics lead unrelated groups of deer to occur closer in proximity, enough so that it leads to between-group contacts.

Currently, managers are trying to mitigate the spread of CWD throughout North America. The Association of Fish and Wildlife Agencies created a document to aid managers in prevention, surveillance, and management of CWD (Gillin and Mawdsley 2018). Several

methods to prevent introduction of CWD include banning of baiting and feeding of deer, preventing movement of cervid carcasses and tissues, and regulating movement of live cervids and sale of some urine products (Gillin and Mawdsley 2018). Once CWD becomes established, surveillance and management plans that promote testing for CWD, proper carcass disposal, and appropriate decontamination methods become vital (Williams et al. 2002; Gillin and Mawdsley 2018; Thompson et al. 2023). Two strategies used to help slow spread of CWD in populations involves culling and hunting, as these methods can remove infected deer and reduce local deer density, lowering the possibility of prion transmission (Manjerovic et al. 2014; Miller et al. 2020; Miller and Vaske 2023). Wisconsin ceased culling deer in 2007 and witnessed an annual CWD prevalence increase of 0.63%, while Illinois maintained culling measures and noticed no change in disease prevalence (Manjerovic et al. 2014). In Colorado, areas within the state that experienced marked declines in hunting license sales displayed an increase in CWD prevalence rates, while those areas where license sales increased or remained unchanged showed no change in CWD prevalence (Miller et al. 2020). These examples provide support that once CWD is established, culling and hunting play a role in maintaining lower prevalence rates and could help slow pathogen spread.

Given what is known about CWD transmission and dynamics in other states, it is likely that CWD will have long-term population level impacts on Michigan's white-tailed deer (Monello et al. 2014; Edmunds et al. 2016; DeVivo et al. 2017). For example, CWD can lead to increases in deer vehicle collisions and predation, as infected individuals are more vulnerable in their weakened state (Krumm et al. 2005, 2009). On a ranch in Wyoming, Edmunds et al. (2016) concluded that CWD-positive deer were 4.5 times more likely to die than deer that tested negative, suggesting that at high prevalence rates deer populations could decline (Edmunds et al.

2016). Adult white-tailed deer in semi-arid environments were predicted to experience CWD-related mortalities resulting in negative rates of population growth (Foley et al. 2016). These population-level impacts on deer could negatively affect wildlife funding, state economies and threaten recreational hunting (Needham et al. 2004; Vaske and Lyon 2011; Price Tack et al. 2018). The Pittman-Robertson Act generates funds for wildlife conservation through an excise tax on sporting arms and ammunition (Crafton 2019). Declines in hunter license sales and declines in sales of sporting arms and ammunition lead to a decline in wildlife conservation funds. In 2020, federal agencies allocated \$284.1 million to CWD-related management, and state agencies allocated \$28.4 million (Chiavacci 2022). Funding needed to manage CWD will increase as the pathogen spreads throughout the United States.

Large knowledge gaps exist in how supplemental feeding affects group dynamics and associated contact rates, and thus, CWD transmission. Few studies have been conducted on how deer interact with each other at different food sources (food plots, bait sites, natural forage) and what the rates of direct contact are at these congregation sites. Storm et al. (2013) noted that expanding foundational knowledge of how landscape features influence deer congregation and risk of CWD transmission is necessary. One of the many challenges facing managers is trying to understand what factors are having the greatest influence on CWD transmission and if management action can slow pathogen spread.

Few studies have tried to quantify how deer behavior, supplemental feeding, and landscape factors affect deer group size and CWD prion transmission. The agriculture dominated landscape of southern Michigan provides a unique opportunity to observe contact rates among deer and their environment during winter. Here, winter (January to April) corresponds to post-breeding in southern Michigan, a time when deer tend to congregate around food sources (Kjaer

et al. 2008). Quantifying these interactions will provide vital information for epidemiological models that aim to create efficient and effective CWD management strategies. In Chapter 1 of this thesis, my objective was to quantify how deer group sizes in winter were affected by landscape features. I hypothesized that landscape features influenced where deer congregated in winter, but that these relationships may change monthly as food sources deplete and annually as crop fields are rotated.

In Chapter 2 of this thesis, I quantified deer contact rates at bait sites, food plots, and in the surrounding landscape. I hypothesized that bait sites and food plots increase the likelihood of behaviors known to facilitate direct and indirect pathogen transmission among deer. The overall goal of my research was to help wildlife managers understand the role supplemental feeding may play in the transmission of prions and if deer are selecting for landscape characteristics in winter.

Study Area

The research was conducted in a 4,262 km² study area encompassing portions of Clinton, Eaton, Ingham, Ionia, and Shiawassee Counties in southcentral Michigan (Figure 1.1) The study area is almost exclusively privately owned lands and consists of agriculture (68%), forest (22%), and developed areas (9%), with the remainder in open water, emergent herbaceous wetlands, barren land, and deciduous scrub/shrub (Figure 1.1; USDA-CDL 2020). Dominant agricultural crops include corn (*Zea mays*), soybeans (*Glycine max*), alfalfa (*Medicago sativa*), and winter wheat (*Triticum aestivum*) (USDA-CDL 2020, 2021). Small tracts of deciduous forest and hedgerows are interspersed among crop fields. Classification of the regional landscape geomorphology is described as medium-textured ground moraines with rich, loamy soils (USDA-Forest Service 2004). Soil types are classified as Hapludalfs plus Argiaquolls (USDA-Forest Service 2004). Depressions are poorly drained, while moraines are well drained (USDA-Forest Service 2004). Elevation ranges from 195 to 342 m (USDA-Forest Service 2004).

In both years of my study (2021 and 2022) data collection occurred 4 January to 30 April. In 2021, average temperature ranged from -14.0 °C to 17.2°C, while in 2022 it ranged from -13.1 °C to 16.5°C (NOAA 2023). In 2021, the study area received approximately 3.89 cm of precipitation and 26.28 cm of snowfall, with an average snow depth of 8.55 cm (NOAA 2023). Precipitation in the second year was 6.9 cm and 28.95 cm of snowfall with an average snow depth of 4.74 cm (NOAA 2023). During the first field season, there was heavy snowfall in January and February followed by warmer than average temperatures in March and April. The second field season experienced similar amounts of snow, but temperatures remained cooler throughout the field season with more rainfall.

Michigan has a rich history of deer hunting with the season in the Lower Peninsula beginning in mid-September and continuing through January 1. Baiting and feeding of white-tailed deer are banned in the entire Lower Peninsula on both public and private lands (MDNR*b* 2023). The south-central portion of the Lower Peninsula also contains a CWD management zone, and all 5 counties from the study area fall within this zone (MDNR*c* 2023).

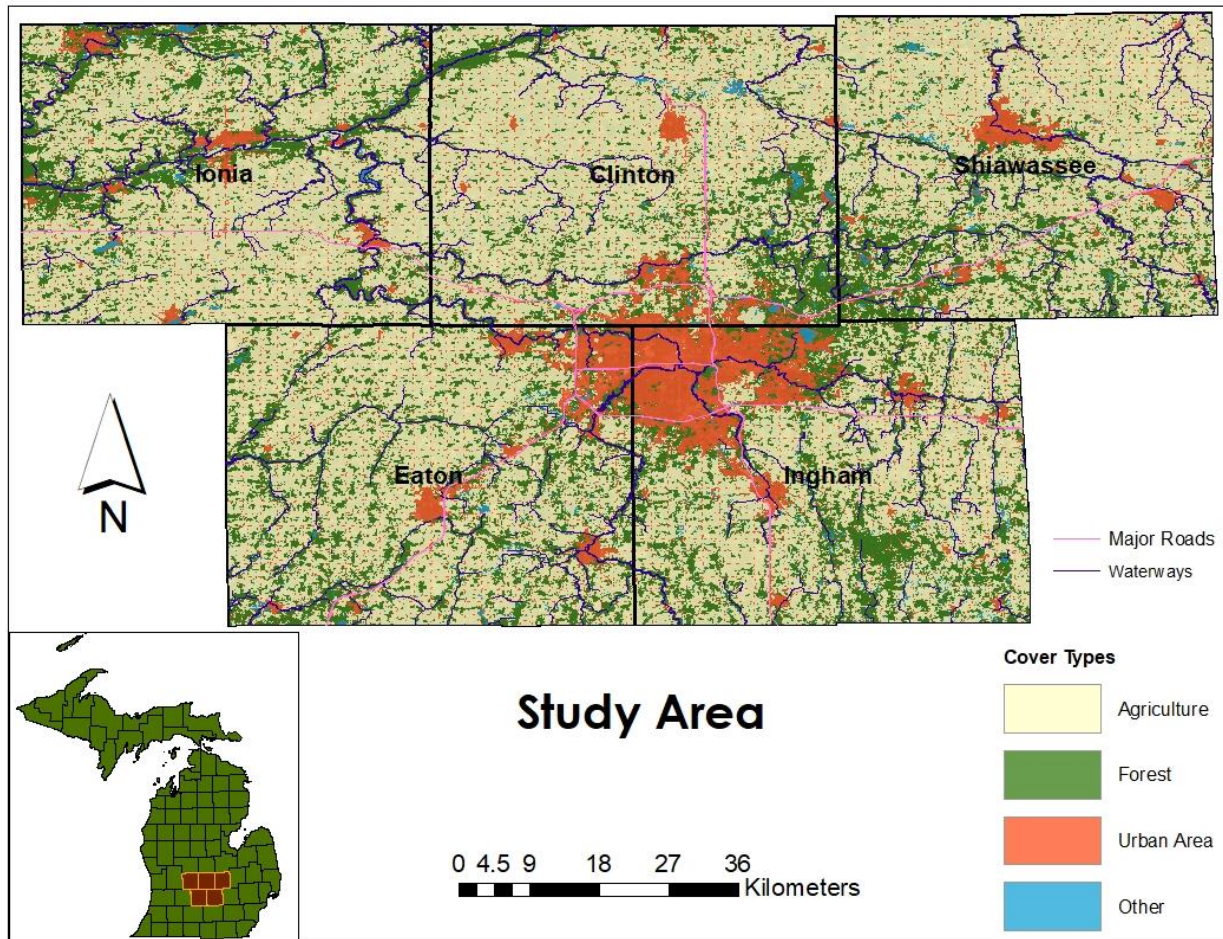


Figure 1.1 The five counties where road-based surveys and camera trapping data were collected in support of deer group size and behavior studies in Michigan from 2021-2022.

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CHAPTER ONE: ENVIRONMENTAL FEATURES AND DEER GROUP SIZE DURING WINTER IN SOUTHERN MICHIGAN: IMPLICATIONS FOR MANAGING CHRONIC WASTING DISEASE

Abstract

Chronic wasting disease (CWD) has been steadily increasing globally since the 1960's and could result in long-term population declines for white-tailed deer (*Odocoileus virginianus*). The potential of direct and indirect transmission of CWD-causing prions increases as deer congregate. Thus, understanding factors affecting deer space use and grouping behavior can help managers identify areas where deer may congregate. My objective in this study was to identify environmental features that influence deer group size to help managers identify areas of congregation, potentially increasing the likelihood of prion transmission. I conducted road-based surveys along 3.5 – 4.83 km long transects from January-April 2021 and 2022, throughout a 4,262 km² area in southern Michigan. I observed 603 deer groups and group sizes ranged from 1 – 67 deer. Total area of corn and forage crops had a positive effect on group size ($\beta=0.12$, 95% CI = 0.02 – 0.22 [corn], $\beta= 0.13$, 95% CI = 0.04 – 0.22 [forage]) with group size increasing by ~1.5 deer across the range of corn measured, and by ~3.5 deer across the range of forage crop measured. Deer group size was larger away from buildings ($\beta=0.09$, 95% CI = 0.006 – 0.18). The global model identified negative associations with residential ($\beta= -0.94$, 95% CI = -1.37 - -0.50) and forest ($\beta= -0.34$, 95% CI = -0.52 - -0.16) cover types on group size compared to agriculture. Contagion had a negative impact on deer group size ($\beta= -0.11$, 95% CI = -0.22 - -0.005), where small forest patches adjacent to agricultural fields corresponded with lower group size. My results indicate that potential areas for larger deer group sizes include larger corn and forage crop fields adjacent to woodlots that are >220m away from buildings. Wildlife agencies can employ appropriate disease mitigation measures as they find these areas on the landscape.

Introduction

Biotic and abiotic factors and landscape features influence deer group size and movements in Michigan. Hirth (1977) noted that deer group sizes and use of open areas in Michigan likely evolved as a predator avoidance strategy (also see Hewitt 2011) or in response to spatial patterns of vegetation growth and structure. Hirth (1977) observed that deer groups were smaller when cover was dense, and groups were larger in open areas absent of cover. Presently, vehicle collisions and hunting are the main causes of deer mortality in southern Michigan (Burroughs et al. 2006; Hiller and Campa 2008), but large predators (e.g., wolves [*Canis lupus*]) have been absent for >100 years, suggesting predator avoidance may no longer influence deer grouping behavior. Little to no vegetation growth occurs during winter in Michigan, so deer are often forced to scrape through snow for forage or browse on woody vegetation (Beier 1987). In agricultural dominated landscapes, deer primarily feed upon agricultural foods and waste grain that remain on the ground post-harvest (Nixon et al. 1991; Hewitt 2011). Hence, access to forage, level of non-predator disturbance, and social bonds likely determine deer grouping behavior during winter in southern Michigan.

Social hierarchy, group size and composition likely play roles in pathogen transmission. A general social hierarchy exists within deer herds, but this can change depending on time of year (Nixon et al. 1991, 1994; Hewitt 2011). Matriarchal groups are most often composed of an adult female, a yearling female, and fawns (Hawkins and Klimstra 1970; Hirth 1977, Mathews and Porter 1993). Group members associate throughout the year, but sexes segregate as pregnant females establish and defend a parturition range in early summer (Hewitt 2011). Female offspring often establish home ranges adjacent to the home range of their mother, varying degrees of overlap depending on season and individual age (Mathews 1989; Nixon et al. 1991;

Porter et al. 1991; Nixon and Etter 1995). Male fawns typically disperse from their mother's range between 1.0 (spring)-and 1.5-years-old (fall; Nixon et al. 1991, 1994). Early dispersing male fawns will join bachelor groups in summer (Hirth 1977; Nixon et al. 1991); however, some yearling males will return to a portion of their mother's range post-breeding season (Nixon et al. 2010). During the breeding season, adult males remain solitary but increase associations with adult females and fawns in winter (Nixon et al. 1991, 1994). Low food availability, overlapping home ranges, and fawns that have not yet parted from their mother may explain why larger groups of deer are observed in winter (Hawkins and Klimstra 1970; LaGory 1986; Beier and McCullough 1990). As group size increases, interaction rates among group members increase because of increased competition for food (Ozoga 1972; Grenier et al. 1999). Adult males have been known to exhibit more aggressive behaviors to replenish body condition post-rut (Nixon et al. 1994; Clutton-Brock et al. 1982), this could potentially lead to an increase in direct contacts among individuals. Annual deer group dynamics likely plays a role in CWD prevalence and persistence. For example, highest prevalence rates of CWD are found in mature males followed by mature females (Farnsworth et al. 2005; Miller and Conner 2005; Gear et al. 2006). Mechanisms for this pattern in CWD prevalence are poorly understood, but because grouping behaviors differ between the sexes (Hirth 1977), directly observing deer behaviors may provide useful insights.

During winter in Michigan, deer shift habitat use and activity in response to snow depth, wind speed, and temperature, opting to utilize wetland and grassland cover types (Beier and McCullough 1990). Large agricultural fields with small tracts of forest dominate the southern and central Michigan landscape. This fragmented landscape provides thermal and escape cover for deer in juxtaposition with a food source (Nixon et al. 1991). Nixon et al. (1988) also found

that deer avoided flood prone woodlands and used wooded pastures absent of livestock. As winter conditions force changes in habitat and food resources, deer congregation areas may shift (Hurst and Porter 2010). My objective was to understand environmental features that determined where deer congregated during the winter and if deer group sizes could be explained from these environmental features. Evaluating these features is vital for creating epidemiological models that can help managers slow the spread of pathogens during a time when deer are congregated.

Methods

Field Methods

To investigate relationships between deer group sizes and landscape characteristics, I observed deer along road survey transects. Within the study area, I used ArcGIS (ArcMap version 10.8.2, Environmental Systems Research Institute, Redlands, California, USA) to randomly select starting and ending locations along secondary rural roads, resulting in 35 transects of 4.83 km each (Figure 1.2). Because major highways and rivers may serve as barriers to deer movements in the region (Locher et al. 2015), I used these features to divide the survey area into 3 areas comprised of multiple groups of transects (Fig 1.2). Prior to the field season, I drove transects to evaluate visibility and safety and replaced transects deemed unsafe (e.g., high traffic volume and speed). Given an estimated annual home range size of 2.25 km² for deer in the region (J. Trudeau, Maryland DNR, personal communication), I attempted to locate transects ≥ 1.6 km apart, thereby minimizing the likelihood of counting the same deer on multiple transects during the same day. Transects were placed into groups of 5-9 to maximize the number of surveys conducted in a day. Transects that could not be located ≥ 1.6 km apart were placed into separate groupings and surveyed on separate days. To reduce transect selection bias, I randomized whether a morning or evening survey would be conducted, region and group to be surveyed, order of transects to be surveyed, and direction of travel. Surveys were conducted 3-6 times per week with morning surveys occurring approximately 15 minutes before sunrise to 2 hours after sunrise and evening surveys occurring 2 hours before sunset to approximately 15 minutes after sunset.

Observers surveyed transects between January and April of 2021 and 2022, corresponding with the end of hunting season and during post-breeding period for deer in

southern Michigan (Christensen 2018). I assumed population closure within each year of sampling given high deer survival and reproduction, and limited dispersal post-breeding (Nixon et al. 2001, J. Trudeau, Maryland DNR, personal communication). Transects were driven in a 4-wheel drive pickup truck at approximately 24 km per hour, while two front seat passengers observed deer from each side of the truck. Conducting surveys at this speed allowed for ideal detection of deer and reduced the potential for double counting individuals (Zamboni et al. 2015, Christensen 2018). Due to Michigan State University COVID-19 protocols, in 2021 only one individual was allowed in a vehicle at a time. To account for this, two trucks were driven separately with the front vehicle acting as the observer and the rear vehicle acting as the data recorder. Observers in both vehicles searched for deer only out of the left side window in 2021, reducing the area sampled compared to 2022.

When deer were detected, observers used binoculars (Leupold BX-2 Acadia 10x42) to identify number of deer groups and number of individuals per group within 457 m of the road. I defined a group of deer as ≥ 1 deer that moved and fed together with individuals separated by $< \sim 50$ m (Monteith et al. 2007). Observers used GPS (Garmin eTrex 20X, Olathe, Kansas, United States) to record the truck location in decimal degrees and measured the radial angle to the center of each group using a planar protractor mounted perpendicular on the vehicle window. Subsequently, observers used a range finder (Vortex Impact 100 Laser) to measure distance (m) from observer to the center of each deer group and spotting scope (Cabela's CX Pro 86mm 20x-60x) to identify sex and age class of each deer within the group. Sex and age classes included adult male (≥ 1 yr old), adult female (≥ 1 yr old), male fawn (< 1 yr old), female fawn (< 1 yr old), unknown sex adult, unknown sex fawn, and unknown sex and age (Hirth 1977; Bowyer et al. 1996).

Observers included graduate students, biologists from the Michigan Department of Natural Resources (MDNR), full-time technicians, and undergraduate student volunteers. I trained all observers prior to surveys using videos and photos accompanied by literature and face-to-face instruction. I conducted practice surveys to train observers to accurately sex and age deer. Volunteers were always accompanied by an experienced observer who assisted with aging and sexing deer. All observational data were collected on a tablet (Apple iPad 6th generation) with the Survey123 software application (ArcGIS 2010).

Quantitative Methods

I used the geosphere package (Hijmans 2022) in R (R Core Team 2023) to estimate geographic coordinates for observed deer groups using angle and distance data collected in the field. At group locations, I extracted crop type using the United States Department of Agriculture Cropland Data Layer for 2020 and 2021 in ArcMap (USDA-CDL 2020, 2021). The USDA CDLs were created using satellite imagery from Landsat 8 OLI/TIRS sensor, the ISRO ResourceSat-2 LISS-3, and the ESA SENTINEL-2 sensors that collect data annually during the growing season (30 m resolution).

To characterize landscape covariates proximal to deer groups I created a buffer around each deer group. Mean post-breeding home-range area for deer in the study area averaged 1.4 km² (SE = 0.11; J. Trudeau, Maryland DNR, personal communication). To assign buffers I applied the radius (r) of a circle representing deer post-breeding home-range +3 SE ($r = 740\text{m}$) to the center of each group. This sized area helped account for deer that may have used slightly larger home-ranges than the documented mean. Buffers for individual groups often overlapped, but Zuckerberg et al. (2020) demonstrated minimal impact on inference in these types of studies due to this overlap.

I used two raster layers (USGS-NLCD, USDA-CDL) to reclassify and evaluate dominant cover and crop types in buffer zones. Using the NLCD layer, I combined all classifications within the planted/cultivated category to create an agricultural cover type. I also combined shrubland and forest classifications (n=5) to create a wooded cover type and the NLCD wetlands classifications (n=2) were combined to form a wetland cover type. Within the CDL layer, I kept corn and soybeans as stand-alone classifications, but reclassified winter wheat, spring wheat, rye, oats, alfalfa, other hay, clover, speltz, and sod into a forage crop category.

Within a buffer, I measured total hectares (ha) of cover type (agriculture, residential, wooded), and crop type (corn, soybeans, forage crop). I used the *landscapesmetrics* package (Hesselbarth et al. 2019) in R to calculate crop and cover type composition, and contagion (CONTAG) within all buffers. Contagion is a measurement of raster cell adjacencies for different cover types; a landscape with many and smaller patch types will have lower contagion than a landscape with larger, contiguous patch types (McGarigal and Marks 1995). I hypothesized that during winter deer forage on leftover crop residue in agricultural fields resulted in a positive influence on deer group size, as these areas offer food while allowing clear sightlines to spot potential predators (Nixon et al. 1991; Hewitt 2011). I also measured distance from each group location to buildings using US Building Footprint (Microsoft 2022) layer without the spatial constraint of the buffer to investigate a potential relationship between group size and anthropogenic presence.

A suite of variables (contagion (CONTAG), edge density, interspersed/juxtaposition (IJI), length of road, nearest distance to building, total hectares of forest, agriculture, wetland, and residential cover types, total hectares of corn, soybean, forage, and other crops) were assessed for my original model. I first used a Spearman's rank correlation test and identified

collinearity among variables. Edge density, IJI, total hectares of wetland, and total hectares of other crop all presented moderate to strong correlations with other variables (Appendix; Figure A.1.1). After removing these variables, I created a global model using year, total length of road, CONTAG, nearest distance to building, total hectares of agriculture, residential, and forest cover types, and total hectares of corn, soybean, and forage crops. After running this model, two variables, length of road and total hectares of soybeans, were deemed unimportant (i.e., 95% CI overlapped 0) and removed from the global model.

I used generalized linear mixed modeling (GLMM) to explore the effects of landscape variables on deer group size. I used the “lme4” package in R (Bates et al. 2015). I specified a truncated negative binomial distribution because 0 for the response variable (i.e., deer group size) was excluded and to help account for overdispersion. Predictor variables included year of observation, cover type where a deer group was observed (i.e., agricultural, residential, wooded), nearest distance to a building, contagion (CONTAG), and amount of corn (ha), forage crop (ha), and soybeans (ha) within a buffer (Table 1.1). Prior to running the model, nearest distance to building, CONTAG, corn, and forage crop parameters were scaled and centered. I also included transect ID as a random effect to account for potential observations of the same deer groups on temporally replicated surveys on a given transect. I used a variance inflation factor (VIF) test to assess multicollinearity in the final predictor variables and assessed model fit using residual diagnostics (Kie et al. 2002).

Results

From January-April of 2021, observers conducted 346 road surveys on 26 transects and observed 182 deer groups and 1,312 deer. Each transect was surveyed an average of 15 times (SE = 0.52). Deer group sizes ranged from 1-47 (median = 5; Fig. 1.3). In 2022, observers conducted 351 road surveys on 34 transects identifying 421 groups including 3,372 deer. Each transect was surveyed an average of 12 times (SE = 0.58). Group sizes ranged from 1-67 individuals (median = 6; Fig. 1.3). Out of 603 groups observed, 1% were bachelor groups, 13% were mixed sex and age (adult males, adult females and fawns of both sexes), and 86% consisted of adult females and fawns of either sex (matrilineal groups). Land cover surrounding group locations was primarily agricultural cover types (64%), followed by forest (25%) and wetlands (11%) (Table 1.2). Within agricultural cover types, soybeans (23%) and corn (22%) were the primary plantings followed by forage crops (12%; Table 1.2).

The VIF function for the global model indicated low correlation among variables (median VIF = 1.13, range = 1.05 – 1.28). Diagnostics on the global model indicated that the residuals were normally distributed (i.e., QQ plot residuals) with residuals randomly distributed around the 0.50 line with no obvious outliers (i.e., Residual vs predicted; Figure A.1.2). The global model identified year (2022) as having the strongest positive effect on group size ($\beta = 0.25$, 95% CI = 0.07 – 0.43; Table 1.3), where group sizes were larger in 2022 than 2021 (Fig. 1.4). Total area of corn and forage crops also had a positive effect on group size ($\beta = 0.12$, 95% CI = 0.02 – 0.22 [corn], $\beta = 0.13$, 95% CI = 0.04 – 0.22 [forage]; Table 1.3) with group size increasing by ~1.5 deer across the range of corn measured (Fig. 1.5), and by ~3.5 deer across the range of forage crop measured (Fig. 1.6). Deer group size was larger away from buildings ($\beta = 0.09$, 95% CI = 0.006 – 0.18; Table 1.3), with average group size increasing by ~3 deer across the range of

distances measured (Fig. 1.7). On average, groups were ~221 meters from buildings (SE = 5.5).

For cover types at the group location, the global model identified negative associations with residential ($\beta = -0.94$, 95% CI = -1.37 - -0.50) and forest ($\beta = -0.34$, 95% CI = -0.52 - -0.16;

Table 1.3) cover types on group size compared to agriculture (Fig. 1.8). Contagion had a negative impact on deer group size ($\beta = -0.11$, 95% CI = -0.22 - -0.005; Table 1.3), where more interspersed cover types corresponded with lower deer group size (Fig. 1.9).

Discussion

I quantified the effects of environmental features on deer group sizes to identify areas on the landscape where deer congregate in larger groups. Deer group size is relevant to disease management because larger groups of deer can potentially increase the likelihood of CWD transmission via direct animal to animal contact, or indirectly via prion deposition or uptake in the environment. I concluded that area of corn and forage crop positively correlates with deer group size. I also found a negative correlation between deer group size and distance to residential buildings. Lastly, I observed smaller deer groups in areas where land cover composition was more homogenous. Recognizing landscape-level patterns in deer grouping behavior can facilitate allocation of resources by managers to more effectively control disease outbreaks. These findings are constrained to crepuscular hours, potentially biasing inferences made regarding group sizes. However, these times of day are when deer are most active (Kammermeyer and Marchinton 1977) and spend more time foraging (Schmitz 1991).

Median group sizes of 5 and 6 in 2021 and 2022, respectively, likely represented individual families of deer. Nixon et al. (1991) found that mothers, their yearling daughters, and their fawns, were the most common groups observed in winter on a 600-ha refuge in east-central Illinois, and white-tailed deer groups in southern Alberta, Canada showed similar patterns in winter (Lingle 2003). In Illinois, female white-tailed deer fawns shared most of their mother's home range if they did not disperse in spring, and the following winter these same related individuals shared ~50% of their mother's range as yearlings (Nixon et al. 1991, 2010). Because of these familial associations, deer have a higher likelihood of contracting pathogens from an infected individual within their family group than from an infected individual outside of the family group (Gear et al. 2010). Using proximity telemetry collars, Schaubert et al. (2015) found

that white-tailed deer in Illinois have considerably higher direct contact rates within family groups than between family groups, and group membership effects on direct contact rates was strongest in winter. It is likely that pathogen transmission in the study area occurs at small, localized spatial scales that correspond to areas used by family groups. Removal of entire family units creates voids in an area that are not reoccupied by adjacent females for several years (Porter et al. 1991; McNulty et al. 1997; Oyer and Porter 2004) and this may be an effective management strategy to slow transmission of CWD prions.

During winter, 26 radio-marked female deer in Illinois used forage crops and corn fields more often than other available crops (Nixon et al. 1991) and I observed a group size increase of 1.5 and 3 deer as area of corn and forage crop increased, respectively. Group sizes I observed in corn (7-8 deer) and forage crops (8-9 deer) likely represented multiple family groups foraging in the same field (Nixon et al. 1991, 2010; Porter et al. 1991; Schaubert et al. 2015). Adult female white-tailed deer have high site fidelity and tend to establish home ranges adjacent to their mother, often creating home range overlap (Marchinton and Hirth 1984; Nixon et al. 1991, Nixon and Etter 1995; Porter et al. 1991). In Wisconsin, winter forage that congregates deer and potentially increases contacts among family groups can facilitate CWD persistence and prevalence on the landscape (Samuel 2023). The probability of CWD transmission among related female deer within 3.2 km was ≥ 100 fold higher than for unrelated deer in the same area (Gear et al. 2010). Therefore, larger deer group sizes consisting of related and unrelated individuals have a higher likelihood of infection when selecting for certain crops during winter foraging. Working with farmers to reduce forage crops and corn fields in areas with CWD infected deer populations could reduce potential exposures among family groups of deer.

Models suggest environmental transmission plays a greater role in the spread of CWD and population level impacts than previously thought. Almborg et al. (2011) used simulation models to predict that population decline of deer is a function of the environmental persistence and infectiousness of the prion. Penned deer became infected with CWD when exposed to contaminated fomites (Mathiason et al. 2009), even in areas that had been decontaminated (Miller et al. 2004). Hamsters (*Mesocricetus auratus*) exposed to plants and prion-bound materials commonly found in urban areas (i.e., wood, cement) became infected through direct and indirect transmission routes (Pritzkow et al. 2015, 2018), and higher prevalence rates of CWD in adult males could be explained by higher food intake from contaminated plant material and soil (Potapov et al. 2013). Prion seeding activity is unaffected when infectious feces are subjected to desiccation and only after 7 freeze-thaw cycles is a decrease in seeding observed (Tennant et al. 2020). Although prion levels in deer feces are lower compared to other bodily fluids, how prions deposited via feces or saliva react to the natural environment and bind to soil likely has management implications (Mathiason et al. 2006; Henderson et al. 2017). As deer excrete fluids, defecate, ingest plants, and interact with natural and anthropogenic materials risk of infection increases. Management of CWD is thus complicated by prion deposition and decay of infected carcasses, thereby contaminating areas and exposing individuals to the pathogen. Although much attention has focused on direct transmission among family members as the primary pathway for CWD prion transmission (Williams et al. 2014; Schaubert et al. 2015; Tosa et al. 2017), my observations of multiple matrilineal groups feeding in agricultural fields during winter suggests that the potential for environmental transmission of CWD among these groups is high. I found that certain environmental features influenced group sizes of deer. Contagion is a measurement of patch type composition, configuration, and spatial distribution of patch types

(McGarigal and Marks 1995). A higher CONTAG value reflects landscapes that have fewer and larger contiguous patches of cover types showing more even distribution and less clumping, whereas lower CONTAG values represent landscapes with smaller, aggregated, and less interspersed patch types. In my study, lower CONTAG scores were associated with significantly larger group sizes, indicating that deer likely congregate in small forest patches that provide cover with easy access to feeding areas in adjacent agricultural fields (Fig. 1.9). This likely increases deer abundance in smaller forest patches, increasing potential contact rates and prion deposition (Smolko et al. 2021). Additionally, Samuel (2023) identified highest CWD prevalence growth rates in areas of Wisconsin consisting of 40% forest cover associated with small agricultural fields, and lowest prevalence growth rates in regions composed predominately of agriculture with only 10% forest cover. If deer group size plays an important role in transmission of the pathogen, then I would predict that CWD would spread slowly across southern lower Michigan because 68% of the landscape consists of agriculture with only 22% forested (see Fig. 1.1).

Roe deer (*Capreolus capreolus*) in southern France had smaller group sizes in areas close to human activity, actively avoiding these areas (Hewison et al. 2001). Additionally, deer in an suburban landscape in Illinois tended to avoid and select for areas further away from dwellings during winter (Storm et al. 2007). However, Swihart et al. (1995) found that white-tailed deer in Connecticut adapted to human presence, observing that 67% of houses in their study area had been visited by deer, likely because of feeding activity and plant species richness near dwellings. I found that deer group size was negatively associated with residential development compared to agriculture, and group sizes increased with distance from dwellings. Most of my rural study area was divided into roaded sections and houses were primarily built along roads. Given this

landscape configuration, it is possible that vehicle traffic associated with houses disturbs deer (Sawyer et al. 2006; Meisingset et al. 2013), causing some individuals to flee and affect overall group sizes. My results suggest that wildlife managers working at controlling CWD will find larger groups of deer for culling further from residential buildings.

My finding that individual or multiple matrilineal family groups were most frequently encountered during winter in the study area has implications for targeted culling. Reducing deer abundance in CWD-positive areas with high animal density is an Association of Fish and Wildlife Agencies recommendation to manage CWD prevalence (Gillin and Mawdsley 2018). Removing female deer is desired for population reduction, and sharpshooting is an effective method for selective deer harvest (DeNicola et al. 1997; Frost et al. 1997; Doerr et al. 2001; Hygnstrom et al. 2011). Miller and Vaske (2023) surveyed all 50 U.S. states and received responses from 38, and of the states with CWD at the time of the survey 32% used sharpshooting to manage CWD and 41% were considering sharpshooting. Some agencies, including MDNR, will respond to new positive CWD cases with targeted sharpshooting to slow disease spread as soon as possible (Uehlinger et al. 2016). While this practice may be an effective tool for maintaining low prevalence of CWD in some areas (Manjerovic et al. 2014), because deer populations have an established social hierarchy and female groups are led by a matriarchal doe (Nixon et al. 1991; Porter et al. 1991), removing adult females may alter herd behavior and movements, potentially resulting in more diffuse space use by remaining deer. In one study, larger groups of deer were allowed to dissipate prior to sharpshooting to prevent unharvested animals from becoming educated to the tactic (Williams et al. 2008). Also in this study, 91% of an enclosed deer herd was removed, resulting in an increase in home range size as deer sought to restructure their social groups (Williams et al. 2008). In Virginia, orphaned male fawns were

more likely to stay near their natal ranges than non-orphaned males; however, orphaned males had larger seasonal ranges overall compared to non-orphaned males (Holzenbein and Marchinton 1992). In west-central Illinois, 9 of 13 (67%) orphaned female fawns emigrated while only 35 of 94 (37%) non-orphans dispersed (Etter et al. 1995). Because groups of deer observed during my study were likely intact family groups, targeted removal of adult female deer could have major implications for CWD spread and prevalence. Disease spread via orphaned females could occur over a greater spatial extent as they disperse to new areas and establish or join a new family group, introducing the pathogen into naïve populations and increasing disease prevalence. In these instances, removing the entire family group is likely an appropriate culling strategy. Mature adult males have higher prevalence of CWD (Samuel and Storm 2016; Samuel 2023), however the mechanism driving this higher rate between sexes is still unknown. One explanation could relate to the tendency for orphaned male fawns to remain in the same area (Holzenbein and Marchinton 1992) increasing CWD prevalence at a localized scale.

As deer congregate during the winter, and group sizes get larger as multiple family groups come together, there is an inherent increase in prion deposition and uptake on the landscape. Understanding these patterns and landscape features can help wildlife managers allocate their resources in a more targeted, efficient manner to help stop or slow the spread of disease. For example, state and federal management agencies could work with local farmers to alter farming practices, such as crop rotations, in areas with known positive CWD cases to try and dissipate larger groups of deer. Additionally, 2 N NaOH was an effective treatment for deactivating prions in silt-loam soils (Sohn et al. 2019). Furthermore, culling success could be increased for agencies by focusing efforts in larger forage crop and corn fields adjacent to

woodlots that are >222m away from a building. Knowing this information may save agencies time and money when employing disease management strategies.

Chapter One Tables

Table 1.1 Description and source of covariates used to model winter (January – April) deer group size relative to landscape features in south-central Michigan, USA, 2021-22.

Name	Description	Source ^a
Distance to buildings	Nearest distance (m) to human buildings	Microsoft Building Footprints
CONTAG ^b	Contagion: measure of the degree to which cover types are interspersed and spatially distributed	NLCD, 2020-2021
Area of corn	Total area (ha) of corn in 172 ha buffer	CDL 2020,2021
Area of forage crop	Total area (ha) of forage crop in 172 ha buffer	CDL 2020,2021
Agriculture cover type	If a deer group was observed in an agricultural cover type	NLCD, CDL 2020,2021
Residential cover type	If a deer group was observed in a residential cover type	NLCD, CDL 2020,2021
Forested cover type	If a deer group was observed in a forested cover type	NLCD, CDL 2020,2021
Year (2022)	Year of observation	

^a NLCD (National Land Cover Database; United States Geological Service 2019; CDL (Cropland Data Layer; United States Department of Agriculture 2020, 2021)

^b Contagion parameter analyzed referencing results from Dechen Quinn et al. 2013

Table 1.2 Proportion of land and crop cover within 1.7 km² buffer around deer group centroids during winter (January – April) in south-central Michigan, USA, 2021 and 2022.

Cover type	Proportion (SE)
Agriculture	.64 (0.50)
Soybean	.23 (0.53)
Corn	.22 (0.56)
Forage	.12 (0.41)
Forest	.25 (1.18)
Wetland	.11 (0.38)

Table 1.3 Parameter estimates from a truncated negative binomial mixed model of deer group size relative to local and landscape features in south-central Michigan, USA, 2021 and 2022. Reference cover type for Corn (ha) and Forage crop (ha) was Agricultural (ha). Reference for Year (2022) was 2021. SE = standard error and CI = 95% confidence intervals.

Parameter	Estimate (SE)	95% CI	
		Lower	Upper
Distance to buildings	0.09(0.04)	0.006	0.18
CONTAG	-0.11(0.05)	-0.22	-0.005
Area of corn (ha)	0.12(0.05)	0.02	0.22
Area of forage crop (ha)	0.13(0.04)	0.04	0.22
Residential cover type	-0.94(0.22)	-1.37	-0.50
Forested cover type	-0.34(0.09)	-0.52	-0.16
Year (2022)	0.25(0.09)	0.07	0.43

Chapter One Figures

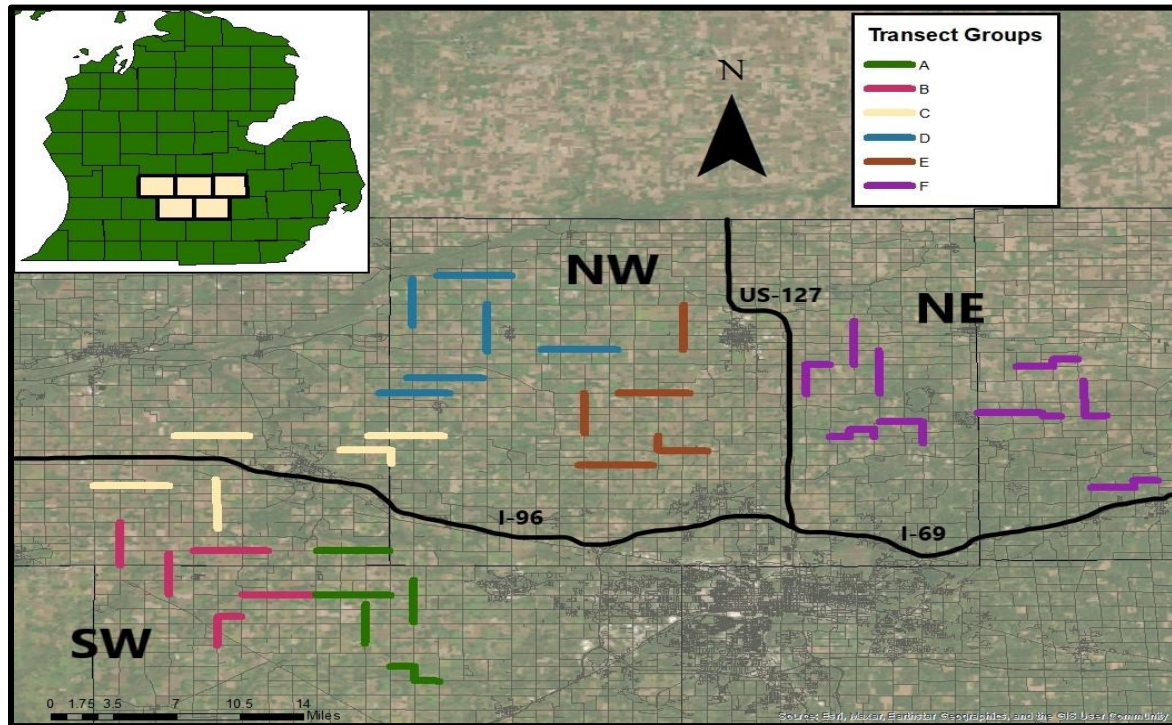


Figure 1.2 Road survey transect groupings divided into regions (NW, NE, and SW) by major highways in south-central Michigan, USA, 2021 and 2022.

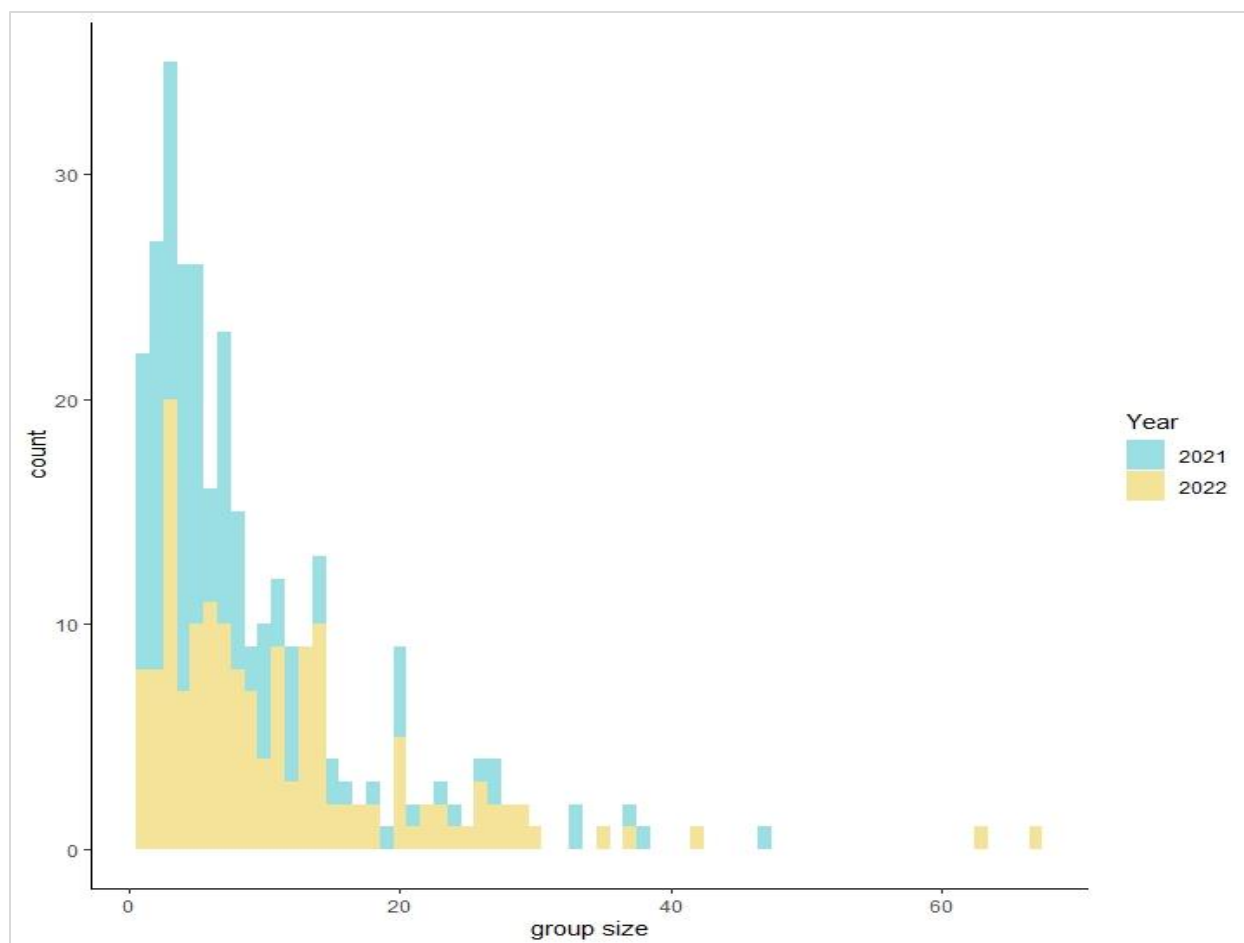


Figure 1.3 Frequency of mean deer group sizes observed along transects in south-central Michigan, USA, during winter season (January – April) in 2021 and 2022.

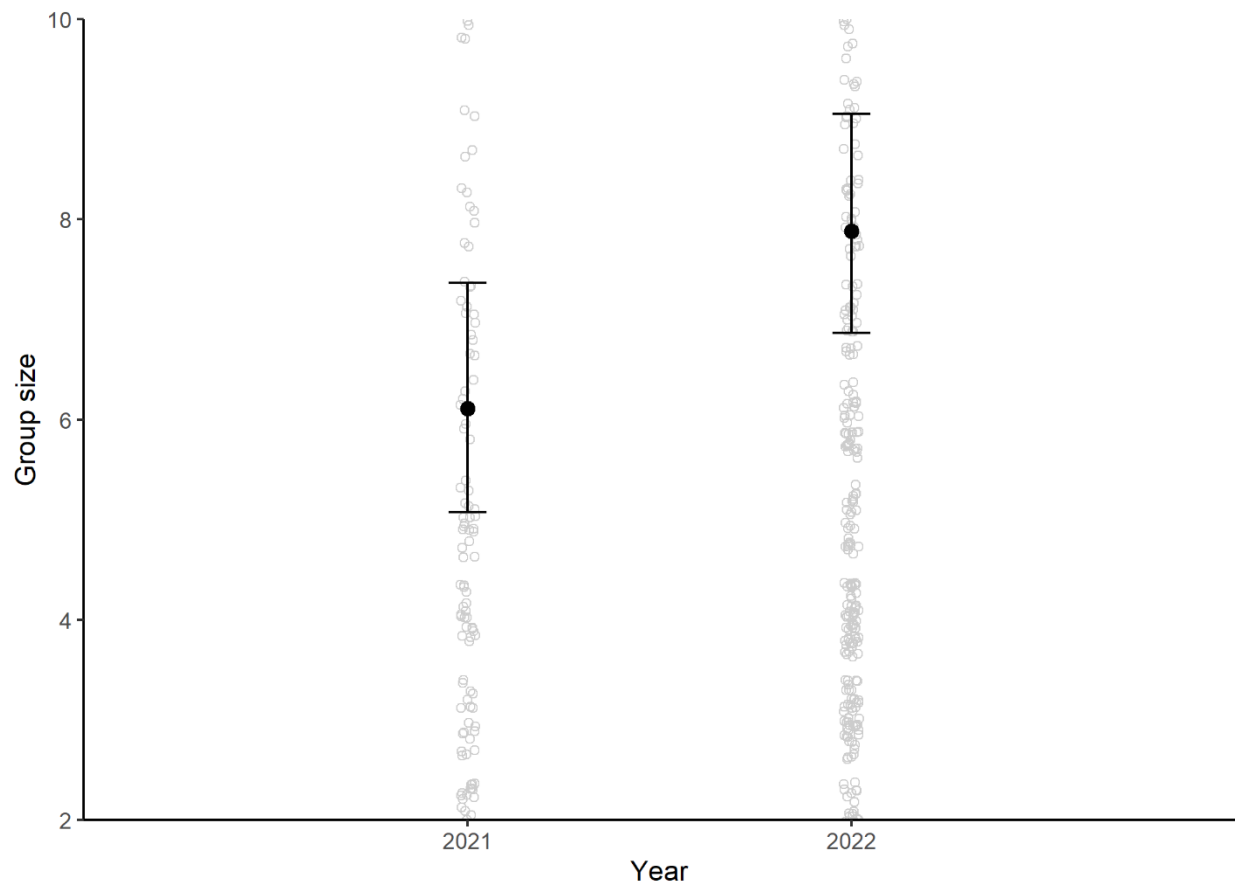


Figure 1.4 Predicted deer group sizes during winter (January – April) in south-central Michigan, USA, 2021 and 2022. Light grey circles indicate data points. Error bars are 95% confidence intervals.

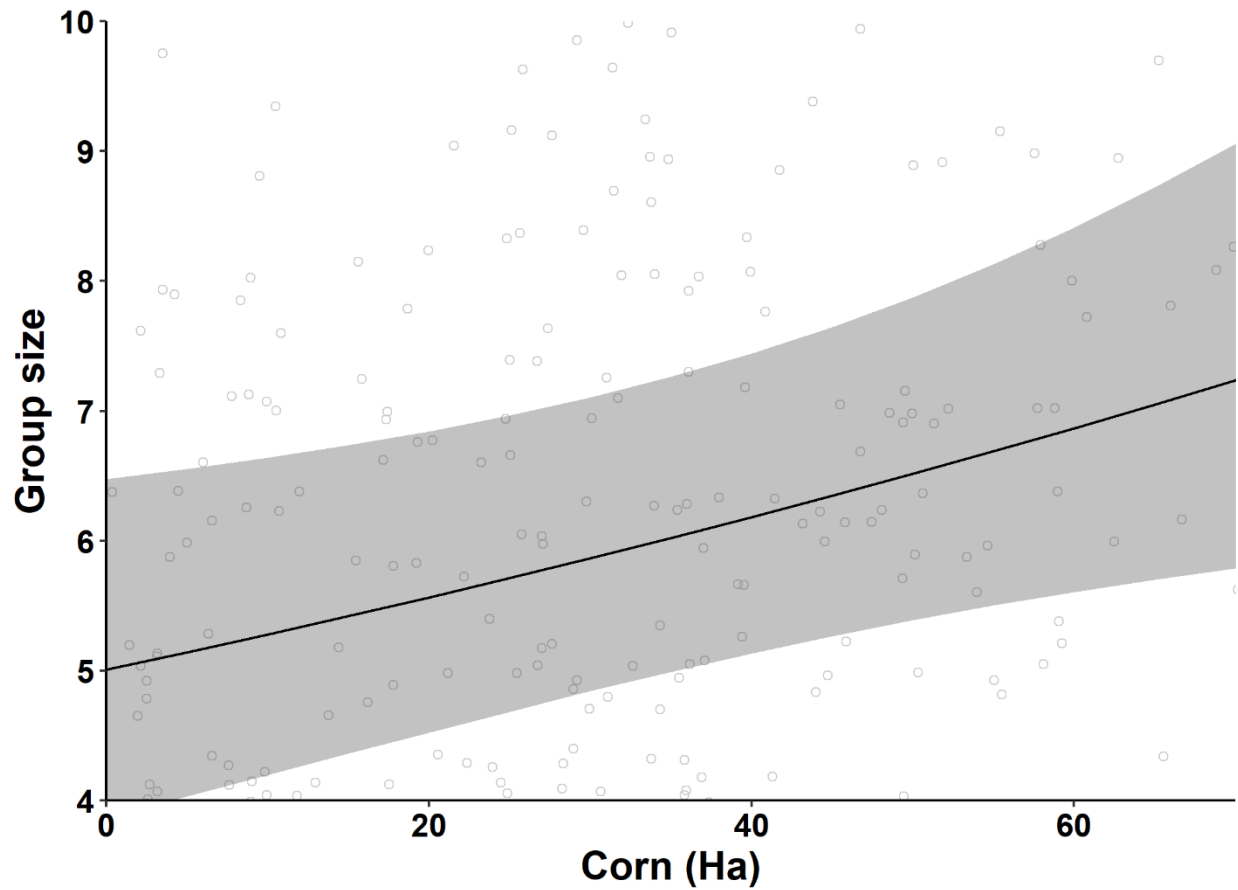


Figure 1.5 Predicted deer group sizes during winter (January – April) associated with corn (ha) within 1.7 km² surrounding deer group centroids in south-central Michigan, USA, 2021 and 2022. Light grey circles indicate data points. Gray shading represents 95% confidence intervals.

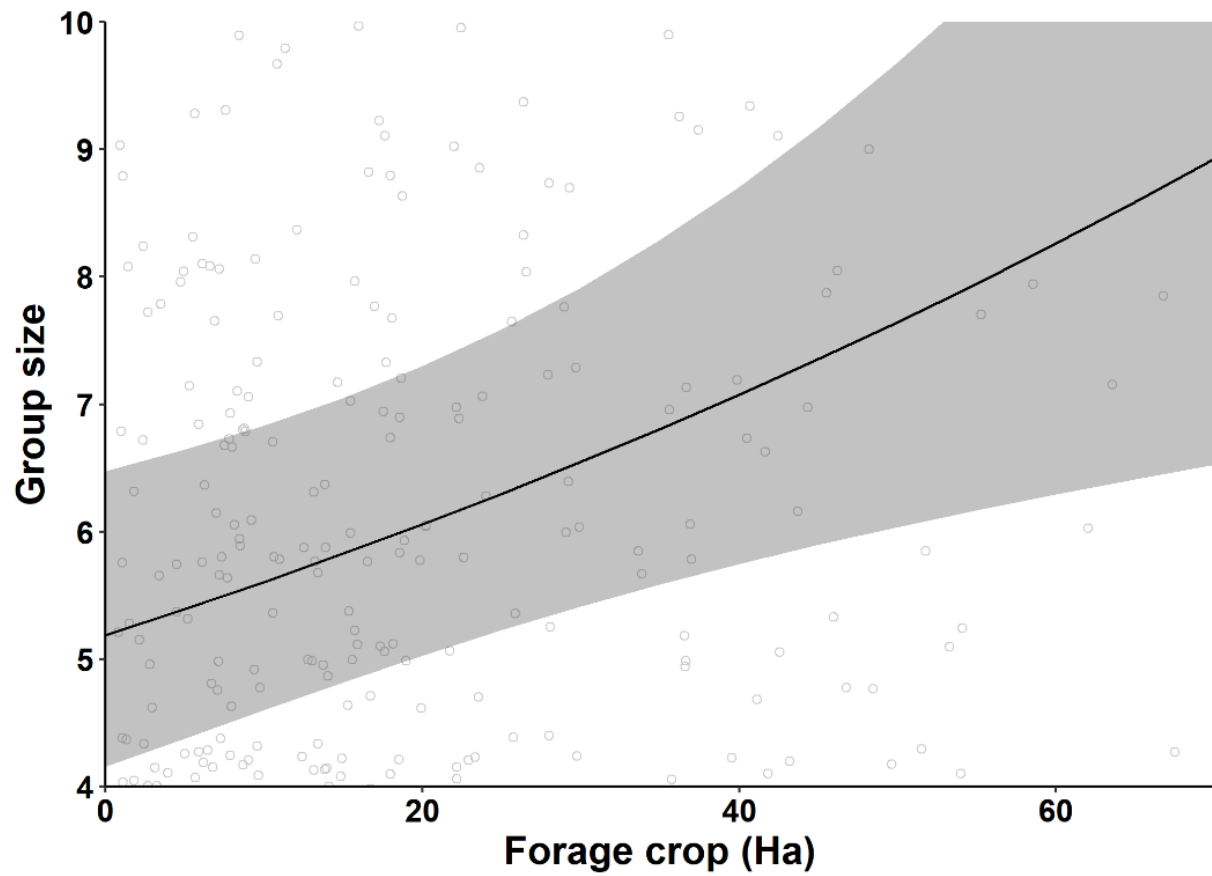


Figure 1.6 Predicted deer group sizes during winter (January – April) associated with forage crop (ha) within 1.7 km² surrounding deer group centroids in south-central Michigan, USA, 2021 and 2022. Light grey circles indicate data points. Gray shading represents 95% confidence intervals.

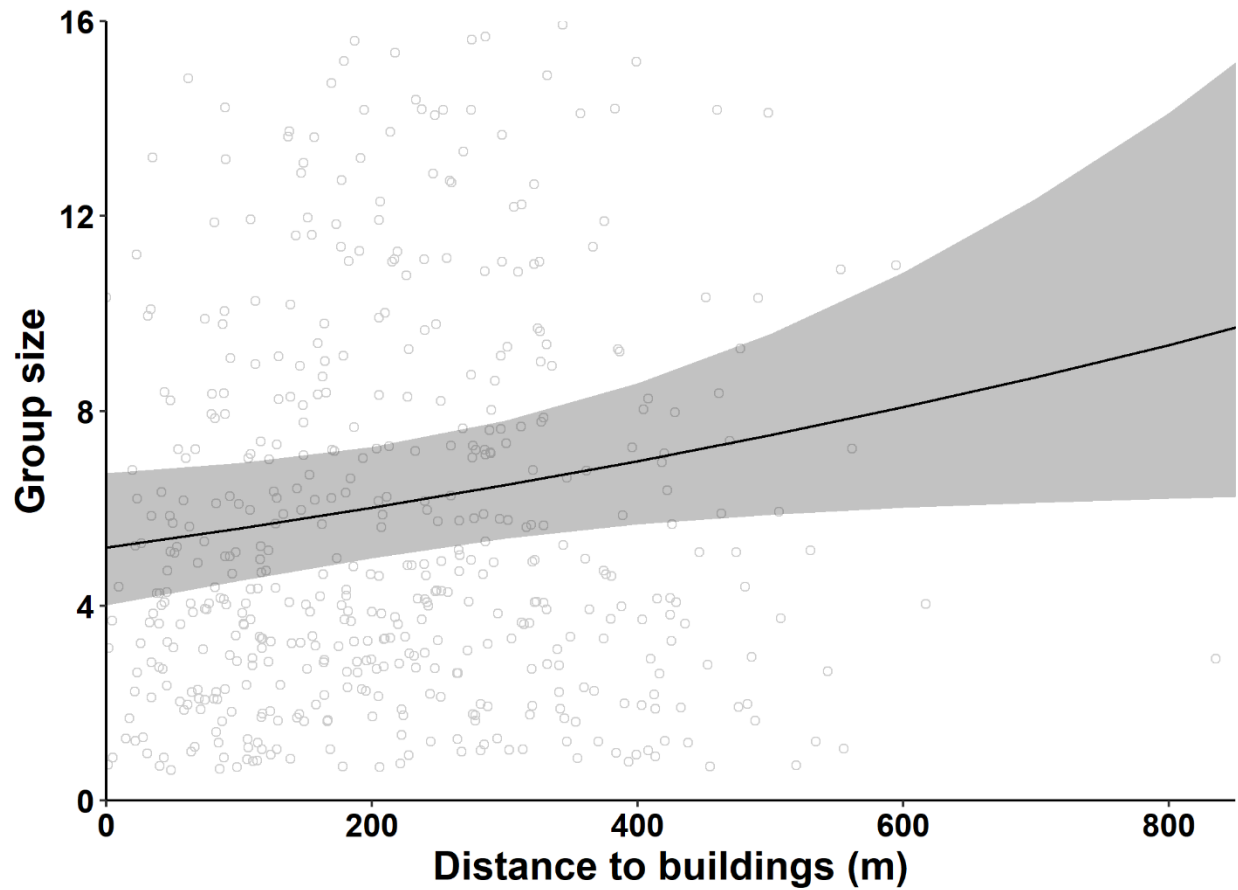


Figure 1.7 Predicted deer group sizes during winter (January – April) associated with the nearest distance to a building in south-central Michigan, USA 2021 2022. Light grey circles indicate data points. Gray shading represents 95% confidence intervals.

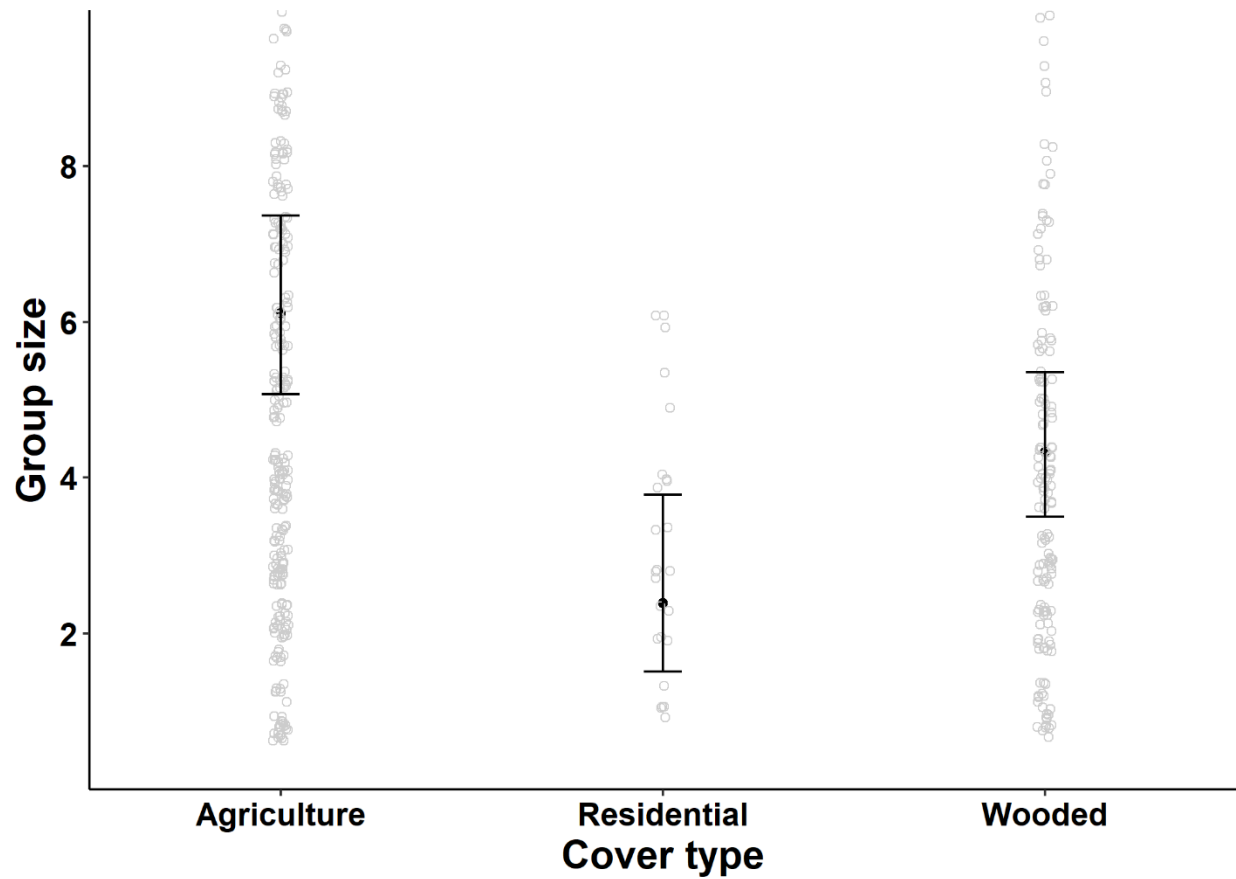


Figure 1.8 Predicted deer group sizes during winter (January – April) for agricultural, residential, and wooded cover types in south-central Michigan, USA 2021 2022. Light grey circles indicate data points. Error bars represent 95% confidence intervals.

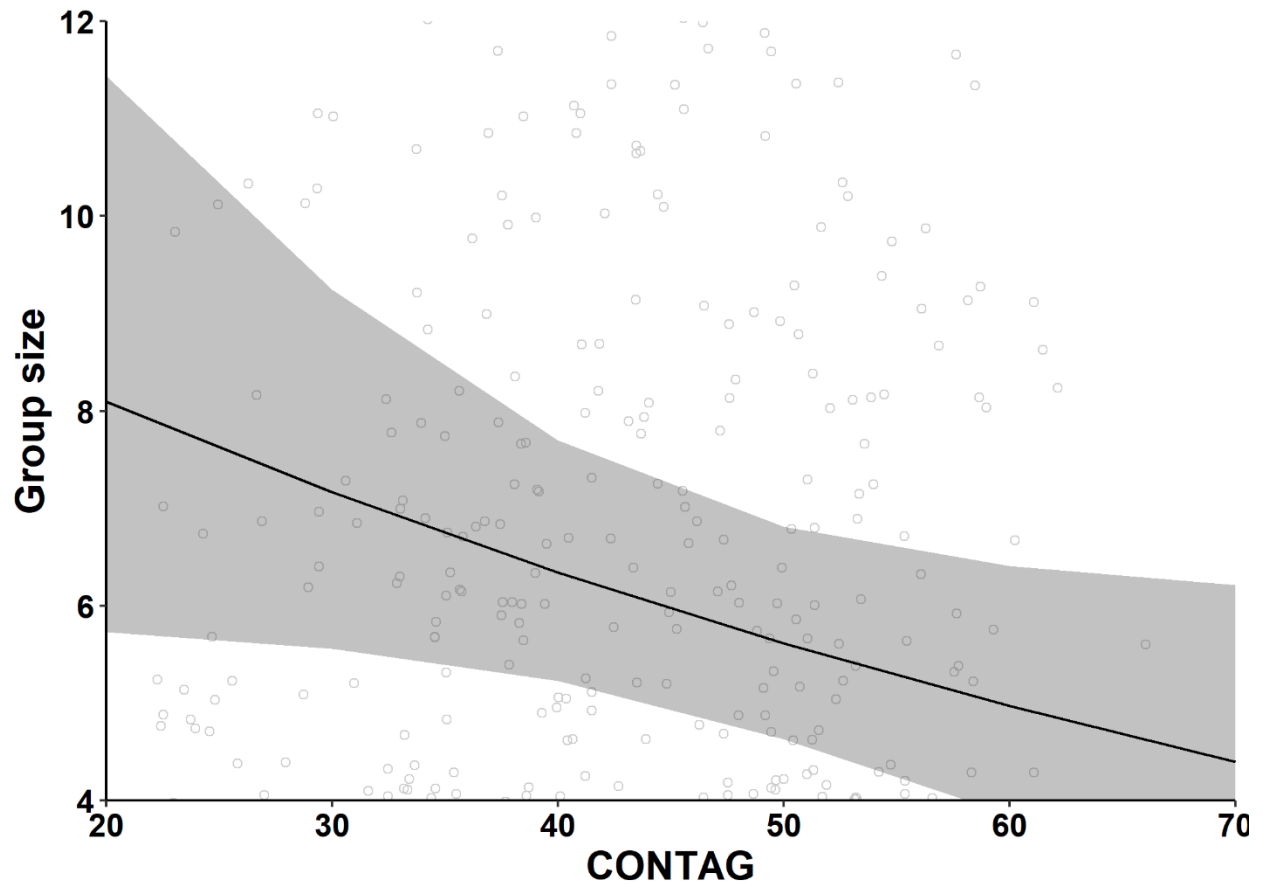


Figure 1.9 Predicted deer group sizes during winter (January – April) associated with contagion (CONTAG) within 1.7 km² surrounding deer group centroids in south-central Michigan, USA, 2021 -2022. Light grey circles indicate data points. Gray shading represents 95% confidence intervals.

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APPENDIX I: FIGURES

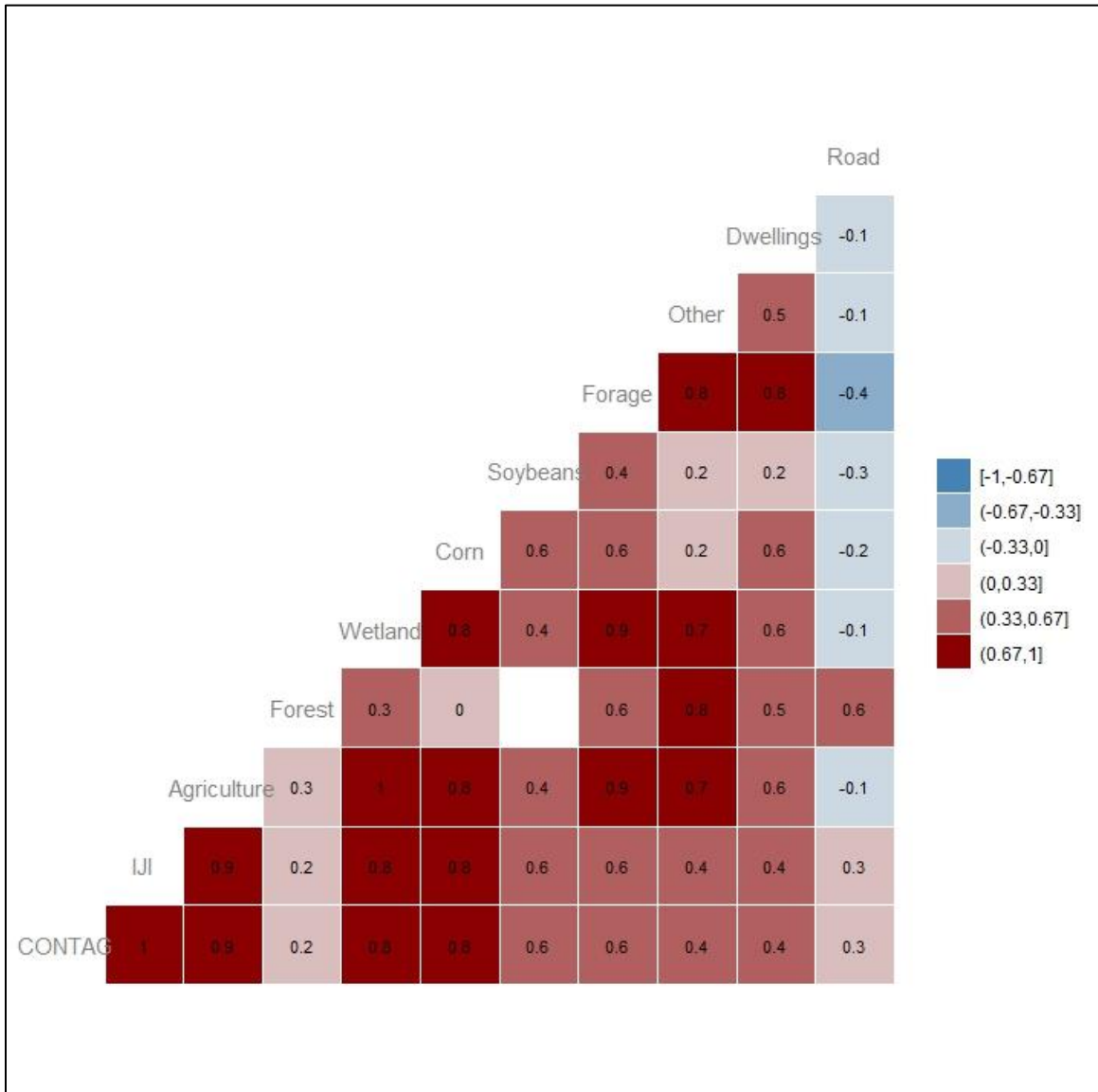


Figure A.1.1 Spearman's rank correlation test for initial model variables (CONTAG (contagion), IJI (interspersation-juxtaposition index), agriculture cover type, forest cover type, wetland cover type, hectares of corn, hectares of soybeans, hectares of forage crop, hectares of other crops, nearest distance to dwellings, and total length of road). Values 0 - -.2 and 0 - .2 indicate a weak or non-existent correlation between variables.

DHARMA residual

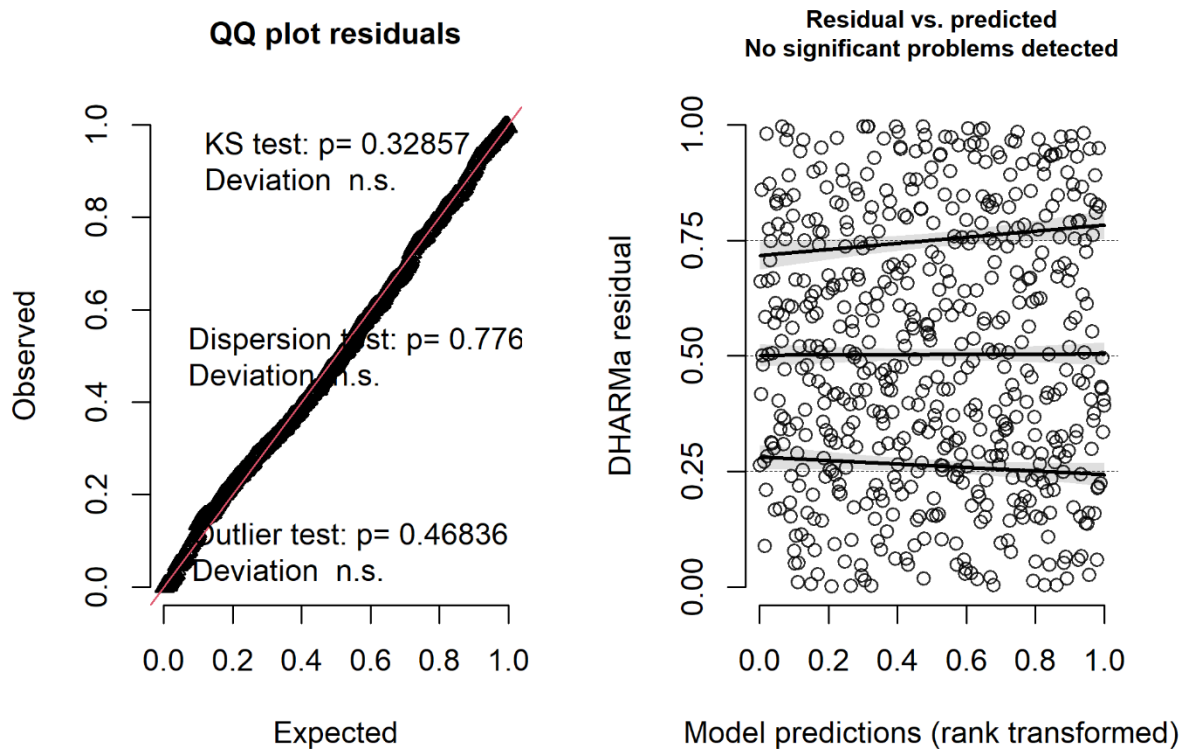


Figure A.1.2 Quartile-quartile (QQ) plot of model residuals (left panel) showing observed values on the y-axis and expected values on the x-axis. Residual plot (right panel) showing residual values on the y-axis and predicted model values on the x-axis. Empirical 0.25, 0.5, and 0.75 quantiles depicted by the solid red line (left panel) are compared to theoretical 0.25, 0.5, and 0.75 quantiles depicted by black lines (right panel).

CHAPTER TWO: WHITE-TAILED DEER BEHAVIORS AT FEED SITES, FOOD PLOTS, AND THE SURROUNDING LANDSCAPE WITH IMPLICATIONS FOR MANAGING CHRONIC WASTING DISEASE

Abstract

Previous studies made assumptions of how frequently deer come into direct physical contact based on proximity of radio-collared individuals, but this information is not precise and does not account for potential contacts among uncollared deer. Other deer behaviors likely play a role in transmission of prions, so I created three behavioral categories (i.e., direct contact, self-contact, environmental contact) to portray a broader range of behaviors potentially linked to prion transmission. My objective was to quantify behaviors exhibited by deer at congregation areas including baited sites, food plots, and naturally occurring forage. I used camera trapping on privately-owned lands and road-based transect surveys (surrounding landscape) during the post-breeding period (January-April 2021 and 2022) to quantify deer behaviors among various sex and age classes. I compiled 395 observations of known sex-age deer during road-based surveys and conducted 2,047 observations from video surveys (bait sites = 1,631, food plots = 416). For all deer observed, I detected significantly fewer direct contacts at food plots ($\beta_{\text{Food plot}} = -1.45$ [95% CI = -2.00 - -0.90]) and transects ($\beta_{\text{Transects}} = -1.12$ [95% CI = -1.64 - 0.59]) compared to bait sites. I found a lower number of self-contacts at food plots compared to bait sites ($\beta_{\text{Food plot}} = -1.14$ (95% CI = -1.64 - -0.64)). I observed fewer environmental contacts at food plots ($\beta_{\text{Food plot}} = -0.68$ (95% CI = -0.90 - -0.47)) and transects ($\beta_{\text{Transects}} = -0.65$ (95% CI = -0.87 - -0.43)) compared to bait sites. My results indicate that the likelihood of direct and environmental contacts at bait sites exceeds contacts at food plots and naturally occurring forage. In areas of CWD concern, food plots and naturally occurring forage offer a less risky food source for deer.

Introduction

Direct contact rates among deer is a vital parameter for modeling CWD and models that incorporate contact rates among deer are highly sensitive to this parameter (Belsare and Stewart 2020; Kjaer and Schaubert 2022). Agreement on what constitutes a direct contact between individual deer is lacking, with most studies based on proximity loggers and GPS collars to estimate contact frequency and duration (Walrath et al. 2011; Lavelle et al. 2014; Tosa et al. 2015). Direct contacts are presumed to occur when two proximity loggers communicate (Walrath et al. 2011), if GPS collars were <25 m apart (Kjaer et al. 2008), or proximity loggers were ≤ 1 m away from each other (Tosa et al. 2015). Lavelle et al. (2014) estimated daily contacts rates for GPS collars were 0.12, 0.66 for proximity collars, and 0.29 from video collars. Walrath et al. (2011) found proximity loggers had a greater mean probability of detecting an encounter between deer compared to direct observations. Additionally, location error from GPS collars and proximity loggers may influence estimates of contact rates due to collar orientation (D'eon and Delaporte 2005), radio transmission power, distance between loggers, animal body mass and fine-scale movements (Ossi et al. 2021). Given the importance of direct contacts for prion transmission in CWD models, and disparity among techniques used to estimate contact rates (Habib et al. 2011; Creech 2011; Creech et al. 2012; Williams et al. 2014), it is imperative to have reliable estimates of direct contacts among deer. Using direct observations to evaluate contact rates and the nature of interactions among individuals is critical for understanding prion transmission, especially during winter and in settings where deer tend to congregate (Nixon et al. 1991).

In the Midwest United States, food habits of white-tailed deer change by season. In winter and early spring, deer rely heavily on browse (leaves and stems of woody plants), forbs,

and crop residue following fall harvest (Korschgen 1962; Nixon et al. 1991). During January-March, daily forage intake and metabolic rates decrease, then begin to increase in April as adult does reach parturition, however, the timing can change depending on seasonal weather conditions and green-up (Moen 1978). During winter, deer are naturally congregating and food resources are limited, potentially increasing competition and likelihood of pathogen transmission as deer come into more direct contact (Grenier et al. 1999). Human activities that congregate deer unnaturally (including baiting, feeding, and the implementation of food plots) remain popular in North America (Miller and Marchinton 2007) and pose risks for increased CWD transmission through both direct and indirect pathways (Miller et al. 2003; Rudolph 2012).

Feeding is the act of providing food materials that might attract deer for various purposes. Feeding can include recreational feeding and supplemental feeding. For recreational feeding, food is provided to improve recreational wildlife viewing opportunities. Supplemental feeding refers to producing food that will attract deer to aid in hunting, or to provide an additional food source, usually in the form of food plots (MDNRa 2023). Baiting is the act of feeding deer to attract them to a specific location, originally used by hunters to increase harvest success (Garner 2001). Common types of bait include corn, apples, salt, and hay (Naugle et al. 1995). Researchers also utilize baiting to attract individuals to accomplish study objectives, such as trapping for radio-collaring (Thompson et al. 1989; Campbell et al. 2006). A survey amongst Michigan deer hunters in 2017 concluded that over 50% of the participants used baiting to improve harvest success or see more deer during hunting (Frawley et al. 2018). Research broadly shows that baiting deer has a marginal impact on overall hunter success rates; however, baiting can increase the success rate in areas where natural food sources are limited (Langenau et al.

1984; Winterstein 1992; Weckerly and Foster 2010). This presents a conundrum for wildlife managers who seek to maintain a balance of disease mitigation and appeasement of stakeholders.

Baiting and feeding provide an unnatural food source and increased nutrition for deer outside of natural forage at certain times of the year. White-tailed deer shift core areas of activity closer to bait sites and will frequently use bait sites that are within their home ranges, but deer are less likely to shift or expand their home ranges to access bait sites (Kilpatrick and Stober 2002; Campbell et al. 2006; Beaver 2017). Peterson and Messmer (2011) found an increase in deer bed sites near areas where active baiting was occurring, providing evidence that deer will alter behaviors, movements, and space use to utilize bait. Deer presumably bed closer to food sources to conserve energy, thus increasing energy stores. This is particularly critical in northern climates during times when food is scarce or environmental conditions are harsh and deer must expend energy to find sufficient food to survive winter. While there are some benefits, deer are in closer proximity to each other for longer periods of time at bait sites, creating a potential increase in disease spread through direct physical and environmental contacts.

Another technique for supplementally feeding deer commonly used by hunters and wildlife managers are food plots. Two primary reasons hunters and wildlife managers use food plots are to aid in hunting and provide a source of food during times of year when natural forage may be scarce or lacking in nutrients (Kammermeyer and Thackston 1995; Tranel et al. 2007). Additionally, food plots are used for recreational viewing purposes and to help mitigate crop depredation (Tranel et al. 2007, Smith et al. 2010). Food plots can be planted in the summer to provide a crop that will attract deer in the fall, or they can be planted in the fall to provide a food source over the winter. Brassica species (*Brassicaceae*), cereal grains (*Gramineae*), clover (*Trifolium*), and corn (*Zea mays*) are commonly used for food plots. Cereal grains, especially oat

and wheat species, are commonly planted for a fall crop. These foods provide nutrition for deer during the rut, they regenerate quickly, and will flush again in the spring (Almy 2019). Brassica species, such as turnips and radishes, are a highly coveted source of energy and nutrition when food is scarce for deer in the winter (Almy 2019). McQueen (2020) found that white-tailed deer foraged in food plots at a higher rate than natural vegetation. Comparable to bait sites, when natural food is limited, deer will forage heavily on food plot vegetation (Sowell et al. 1985). Sowell et al. (1985) found that 27% of mule deer (*Odocoileus hemionus*) winter diets consisted of planted wheat and rye, resulting in increased diet quality. Although there has been research on the efficacy and cost effectiveness of food plots, an extensive literature search produced no evidence of how deer interact at food plots and how this relates to potential pathogen transmission.

Food plots and bait sites may not pose the same level of pathogen transmission risk because of dissimilarities in how deer use the attractant. While baiting causes deer to concentrate in a focal area, such as around a feeder or bait pile, food plots typically extend over broader areas (Kammermeyer and Thackston 1995; Harper 2019). Spreading food across an area may reduce the potential for direct physical contact among deer. While baiting and food plots are commonly used for supplemental feeding, deer behaviors and contacts among deer at each should be assessed separately because of contrasting deer numbers at a given site and duration of foraging activity that may occur within the feed area.

A concentrated food source that is being used by deer leads to unnatural congregation, potentially resulting in more direct physical (i.e., among deer) and environmental interactions. For CWD, only 300 ng of CWD-positive saliva is required to cause infection in deer (Mathiason et al. 2006; Denkers et al. 2020). Deer also can experience indirect environmental contact with

CWD prions through urine and feces deposited on or near remaining feed (Plummer et al. 2017). The level of risk associated with supplemental feed sources via direct and indirect transmission remains poorly understood. I hypothesized that deer in winter would exhibit more direct contacts at bait sites than food plots or the surrounding landscape presumably due to increased food competition in a smaller area. I also hypothesized that adult males would exhibit direct contacts more often than other sex-age groups because of increased nutritional demands following the breeding season (Nixon et al.1994; Clutton-Brock et al. 1982).

Methods

Field Methods

Remote cameras provide an opportunity to observe deer behavior and potential risk of prion transmission at food plots and bait sites. In this study, comparisons to direct observations of deer behaviors along transects in the surrounding landscape served as a control and offered a means to evaluate contact rates among bait sites, food plots, and the surrounding landscape. Baiting and feeding deer is illegal in the Lower Peninsula of Michigan; however, I worked in cooperation with the Michigan Department of Natural Resources (MDNR) who granted an exemption for this research. In collaboration with private landowners, I established 10 bait sites and 8 food plots in 2021 and 10 bait sites and 11 food plots in 2022 (some at the same locations for both years; Fig 2.1). I located bait sites ≥ 3.2 km away from transects and food plots to reduce the possibility of influencing localized deer movements (Skuldt 2005; Thompson et al 2008), and established bait sites in open agricultural fields or cleared shrubland to facilitate placement of remote camera arrays. Several ($n=8$) bait sites were established prior (i.e., 2018 to 2020) to this study for live-deer capture on another research project. Prior to my study, these sites were last baited before 16 March 2020.

The locations of food plots and type of food planted were pre-determined by private landowners several months before data collection. Food plots averaged 8.2 km (range = 3.8 km – 20.4 km) away from bait sites and 3.3 km (range = 0.27 km – 12.3 km) from transects. In 2021, food plots consisted of 1 clover (*Trifolium* spp.), 4 brassica (*Brassica rapa*, *Raphanus sativus*), and 1 winter rye (*Secale cereale*) plot. In 2022, field crews sampled 3 clover, 3 winter rye, and 3 mixed variety plots consisting of clover, rye, and brassica. Food plots varied in size from approximately 4,046 m² to 9,888 m². Given difficulty finding food plots in 2021, I selected two

larger agricultural fields planted with brassica and clover as cover crops to serve as food plots (Fig. 2.1). In these two fields and in the two largest food plots, I set up two camera arrays (Fig. 2.2).

At bait sites and food plots, camera arrays were configured as a pentagon using t-posts at each corner (Fig. 2.2). Each t-post was approximately 11.7 m apart and in the center of the pentagon I positioned 4 PVC pipes in a 9.29 m² square (Fig 2.2). Within the area of the PVC pipes, I followed MDNR regulations for baiting deer in the Upper Peninsula of Michigan (MDNRa) and scattered 7.5 liters of corn evenly across the ground, 2 times per week. I attached Browning StrikeForce HD ProX cameras to t-posts 0.6 m off the ground and facing inward 10 m from the center bait area (Fig. 2.2). I used two cameras to increase effort and detectability of deer. A trail camera was attached to the southeast and southwest metal t-posts, facing northwest and northeast, respectively (Fig. 2.2; Pease et al. 2016). I deployed cameras with AA lithium batteries and configured cameras for a 2-second delay and 2-minute video upon detection of motion. Field crews checked batteries and SD cards at bait sites twice per week and food plots were checked once per week. Sites remained undisturbed by research staff throughout the rest of the survey period to promote deer acclimatization.

Videos from bait sites and food plots were organized by site, date, morning and evening periods, and camera orientation (i.e., northwest and northeast facing). The morning survey period occurred 15 minutes before sunrise and ended 2 hours after sunrise. The evening survey period began 2 hours before sunset and ended 15 minutes after sunset. Any videos recorded outside of dawn and dusk were removed from the sampling pool. When choosing between northeast and northwest facing cameras for analysis, I selected the camera that recorded more videos and then used a random number generator to select 2-min videos from that camera to observe. My goal

was to identify two 2-min video clips per site per day in the morning and evening to standardize observation effort, resulting in up to 16 30-sec segments per day.

I used Survey123 (ArcGIS 2010) to record data on deer demographics, contact rates, and behaviors from videos. I counted the maximum number of deer observed within a 2-min video segment and the maximum number of deer observed within the center square of the camera arrays. Every deer within the video was sexed and aged by trained technicians, if there was any uncertainty, the deer was classified as unknown. I classified sex and age of deer as adult male (≥ 1 yr old), adult female (≥ 1 yr old), male fawn (< 1 yr old), female fawn (< 1 yr old), unknown sex adult, unknown sex fawn, and unknown sex and age (Hirth 1977; Bowyer et al. 1996). Adult males have a higher prevalence rate of CWD, and because they are less observable and exist at lower densities in comparison to other sex and age classes of deer (Zagata and Haugen 1974; Nixon et al. 1991; Gear et al. 2006), I prioritized observing adult males as the focal deer if they were present in the group. Given males shed antlers throughout the time of my research, I used multiple morphological characteristics to sex and age individuals (Geist 1998; Mejía Salazar et al. 2016). If deer did not have visible antlers, technicians looked for pedicels where antlers may have recently detached (Ozoga 1972). Later in the season technicians looked for antler protrusions, where the hair is sometimes a different color directly above the eyes. Male adults and fawns both have blocky foreheads covered by dense hair that can be darker in color. Female adults and fawns have a triangular, flat forehead with shorter hair. If circumstances allowed, technicians were able to observe male genitalia. In the absence of an adult male, I used a random number generator to select a sex-age class of deer to observe from each 2-min video segment.

Within each 2-min video segment, I recorded every unique behavior exhibited by the focal deer within a 30-second segment until the segment ended or the deer exited the video.

Behaviors were categorized into “interactions between deer” (direct contact), “contact with self” (self-contact), and “interactions with environment” (environmental contact; Table A.2.1).

Technicians observed deer for 2-minutes, comprised of up to four 30-second segments, and each categorized behavior was only recorded once per 30-sec sampling segment. For example, if the focal deer pushed another deer in three of four 30-sec sampling segments in a 2-min video, direct contact was recorded as three.

Deer observations along road-based surveys served as a control for how deer behaved in the surrounding landscape. Prior to driving transects each day, field crews used a random number generator to determine the sex-age class and order of deer to observe when adult males were not present. Upon spotting a group of deer and identifying the focal deer for observation, technicians used a spotting scope (Cabela’s Krotos 86 mm 20x-60x) to observe behaviors. The observer communicated to the recorder each time a deer performed a behavior (*sensu* Grenier et al. 1999); however, categorized behavior was only recorded once per 30-sec sampling segment. Each deer was observed for 2 minutes, but on occasion the observer could break every 30 seconds for eye relief. Deer were observed in 30-sec segments until completion of a 2-minute period or until the individual was no longer visible. After completing observations on the first deer, a second individual from the group was randomly selected and the process repeated. Only two deer were observed per group. The protocols were deemed exempt by the Michigan State University Institutional Animal Care and Use Committee as the research was non-invasive and animals were observed undisturbed in their natural habitat.

Quantitative Methods

For each 30-sec segment on a given day, I denoted whether a behavior category (i.e., direct contact, self-contact, environmental contact) occurred as a “1” (else “0”). I then summed

the number of 30-sec segments by type of contact that occurred by treatment (i.e., bait sites, food plots, and the surrounding landscape) at a site on a given day. At most, there was potential to tally 16 (8 in morning, 8 in evening) direct, self, and environmental contacts per day. I used the “lme4” package (Bates et al. 2015) to run a generalized linear mixed model (GLMM) with a zero-inflated negative binomial distribution to predict the likelihood of a behavior category. I included date and treatment type as predictor variables. Camera array location or transect identifier was used as a random effect in the model to help account for repeated observations of the same deer over time. I assessed model fit by checking for overdispersion and generating residual and prediction plots.

I was also interested in the likelihood of direct contacts at bait sites among deer sex-age classes. For each sex-age group I determined if other deer were in the video frame (thus available for contact with the focal deer) and when other deer were available, denoted whether a contact occurred and the contacted sex-age group. I made this assessment for 30-sec video clips. Because the dataset was non-normal, I used a quasibinomial model with a logit function that predicted the likelihood of a direct contact for a focal sex-age group (e.g., adult males) based on the number of deer within the video frame of all sex-age classes (i.e., adult males, adult females, female fawns, and male fawns) as fixed effects. I used a GLMM and specified a penalized quasi-likelihood (GLMM-PQL) distribution using the “MASS” package in R (Ripley et al. 2002). I also included an array-level random effect to account for potential observations of the same deer and groups over time, and year as a fixed effect. This model was evaluated by checking for collinearity and generating residual and prediction plots.

Results

Deer triggered cameras more frequently in the evenings at bait sites and food plots for both years (Table 2.1). From these videos, I observed 6,309 30-sec segments from 20 bait sites and 19 food plots in 2021 and 2022, respectively (Table 2.2). The majority ($n=5,251$) of the 30-sec segments came from bait sites, with the rest ($n=1,058$) at food plots (Table 2.2). This could be attributed to the difference in size between bait sites and food plots. At bait sites, the food is in a small square that attracts deer, but in food plots the food source is spread across a greater geographic extent, not necessarily forcing deer in front of the video camera. Although adult males were given preference during observations, at bait sites 30-sec observations were relatively evenly distributed among adult males (30% of observations), adult females (26%), and male fawns (28%), with female fawns least observed (16%; Table 2.2). The same pattern emerged from food plots, with relatively equal observations among adult males (25%), adult females (28%), and male fawns (28%), followed by female fawns 19%; Table 2.2).

From 26 transects, I observed deer behaviors 131 times in 2021 and 264 in 2022 resulting in 801 30-second segments from known sex-age deer in both years combined (Table 2.2). In 2021, I observed behaviors by adult females most on transects (3% of observations), followed by adult males (25%), female fawns (22%), and male fawns (20%; Table 2.2). In 2022 I observed behaviors more for adult males (33%), followed by adult females (28%), male fawns (22%), and female fawns (18%; Table 2.2).

For 5,251 30-sec video segments collected at bait sites, I observed direct contacts in 15% of the segments and self-contacts in 7% (Table 2.3). I observed environmental contacts in 91% of the 30-sec video segments at bait sites (Table 2.3). Of the 1,058 30-sec video segments recorded at food plots, I observed direct contacts, self-contacts, and environmental contacts in

9%, 3%, and 88% of segments, respectively (Table 2.3). For transects, I documented 8% direct contacts, 11% self-contacts, and 79% environmental contacts (Table 2.3).

For all deer observed and with bait site as the reference treatment (Table A.2.2), I detected fewer direct contacts at food plots ($\beta_{\text{Food plot}} = -1.45$ [95% CI = -2.00 - -0.90]; Fig 2.3) and transects ($\beta_{\text{Transects}} = -1.12$ [95% CI = -1.64 – 0.59]). Diagnostics for this model indicated that the residuals were normally distributed (i.e., QQ plot residuals) with residuals randomly distributed around the 0.50 line, however, several potential outliers were noted (Residual vs predicted; Figure A.2.9) Similarly, I found a lower number of self-contacts (Table A.2.3) at food plots compared to bait sites ($\beta_{\text{Food plot}} = -1.14$ (95% CI = -1.64 - -0.64; Fig 2.3), and no difference in self-contacts between transects and bait sites ($\beta_{\text{Transects}} = 0.04$ (95% CI = -0.39 – 0.48; Fig 2.3). The diagnostics for the self-contact model showed that there was significant deviation within the distribution (i.e., QQ plot residuals) and several potential outliers (i.e., Residual vs predicted; Figure A.2.10). Additionally, more direct and self-contacts occurred as Julian date increased ($\beta = 0.37$, CI = 0.25 – 0.49; Figs 2.4, 2.5, respectively). I observed fewer environmental contacts (A.2.4) at food plots ($\beta_{\text{Food plot}} = -0.68$ (95% CI = -0.90 - -0.47)) and transects ($\beta_{\text{Transects}} = -0.65$ (95% CI = -0.87 - -0.43)) than at bait sites (Fig. 2.3). The environmental contact model diagnostics indicated significant deviation within the distribution (i.e., QQ plot) and significant deviation among quantiles with several potential outliers (i.e., Residual vs predicted; Figure A.2.11).

Sex and Age Specific Behaviors

Direct contacts between individuals facilitate deer-to-deer spread of CWD, hence I was particularly interested in sex-age group direct contact interactions. However, low numbers of direct contacts among some sex-age groups within treatment prohibited modeling of sex-age

interactions for food plots and transects. Thus, I focused modeling on bait sites which had the greatest number of direct contacts (Table 2.3).

For bait sites, models converged for adult males, adult females, and male fawns. No multicollinearity among model variables was identified. Adult males were more likely to exhibit a direct contact when in proximity to more male fawns ($\beta_{\text{Male fawns}} = 0.45$ [95% CI = 0.19 – 0.71]; Fig 2.6B). I also observed more direct contacts by adult males in 2021 than 2022 ($\beta_{2022} = -0.88$ [95% CI = -1.37 – -0.39]; Table A.2.5). Similarly, adult females were more likely to exhibit direct contact in 2021 than 2022 ($\beta_{2022} = -1.31$ [CI = -2.05 - -0.57]; Table A.2.6). Surprisingly, for adult females, I found a decrease in the likelihood of a direct contact occurring when numbers of adult females increased ($\beta_{\text{Adult females}} = -0.43$ [95% CI = -0.78 – -0.09]; Fig.2.6A). For male and female fawns, I found that direct contacts with adult females was more likely as the number of adult females increased (Adult females = $\beta_{\text{Female fawns}} = 0.65$ [95% CI = 0.25 – 1.05]; Male fawns = $\beta_{\text{Female fawns}} = 0.62$ [CI = 0.10 – 1.13]) were present (Fig 2.6C). Like adult males, male fawns showed a strong negative effect for year, with more direct-contacts in 2021 than 2022 ($\beta_{2022} = -0.83$ (CI = -1.47 – 1.13); Table A.2.7).

Discussion

This study is the first to investigate different types of contacts (direct, self, environmental) in a variety of deer foraging areas (bait site, food plot, surrounding landscape) with implications for pathogen transmission. Direct contact has often been assumed as the riskiest behavior to transmit pathogens because of the potential spread of bodily fluids among animals (Schauber et al. 2015). This research documents that direct contact between individuals are rare events; however, I observed more direct contacts at bait sites compared to food plots and the surrounding landscape. Garner (2001) observed in a single winter an average of 28 face-to-face contacts between 2 or more deer at winter bait sites during a sixty-minute period. The following winter an average of 8.5 face-to-face contacts were observed. Cosgrove et al. (2018) modeled the effects of winter supplemental feeding on bovine tuberculosis prevalence and found a 2-3% increase for every 2 months individuals were fed, and a 50% increase after 5 years of winter feeding.

Information on indirect and self-contact rates, and the nature of contacts among multiple individuals (e.g., including unmarked deer) is generally lacking in data collected via GPS collars and proximity loggers. Recently, accelerometers attached to GPS collars have provided information on some indirect or self-contact behaviors (Benoit et al. 2023). Accelerometers attached to free-ranging roe deer accurately (68-94%) portrayed running, walking, and immobile behaviors, but grooming behaviors were only 34-38% accurate (Benoit et al. 2023). Benoit et al. (2023) acknowledged variation in accelerometer performance as signals varied among individuals due to collar tightness and sensitivity. Benoit et al. (2023) also found that accelerometer data were accurate when deer were foraging with their head down, an important environmental contact to observe for indirect pathogen transmission. Video systems attached to

collars also can aid in portraying interactions between individuals and social group structure and dynamics, but this technique was less accurate in estimating contact rates than other methodologies due to battery limitations Moll et al. 2009; Lavelle et al. 2014). Additionally, video collars can capture individuals foraging on vegetation (Lavelle et al. 2012). While several methods may attempt to obtain direct, self, and environmental contacts, they are not without limitations.

I conducted a comparative analysis of direct, self, and environmental contacts at bait sites, food plots, and the surrounding landscape from January-April when deer naturally congregate in agricultural dominated landscapes (Nixon et al. 1991). Deer in winter and spring typically spend >95% of active time foraging (Beier and McCullough 1990), and most deer I observed at all three treatments were actively feeding. The concentration of food varies greatly among bait sites, food plots, and the surrounding landscape. Transects sampled the existing landscape allowing broad spacing among deer while feeding. Food plots were 0.4 – 1 ha in size which allowed limited spacing among deer while feeding. Bait sites were 9.06 m², restricting spacing of deer that wanted access to bait. Male white-tailed deer are known to reduce or shift their core area of activity closer to bait sites, and deer of both sexes increase their use of baited areas (Beaver 2017). In the Upper Peninsula of Michigan, white-tailed deer that were supplementally fed had smaller home range sizes compared to those not fed, and selected for poor quality winter habitat (Petroelje et al. Personal communication). The confined area of a bait site forces deer to contact each other at unnatural rates (Garner 2001; Schaubert et al. 2015).

An unnatural congregation of deer inherently increases risk of pathogen transmission via increased contact and prion deposition, potentially creating infectious reservoirs. Size of a feed site and duration the food is available might influence deer behavior and the risk of pathogen

transmission. While bait or supplemental feed sites can be offered year-round, food plots are typically used in the fall for hunters to attract deer or in winter to augment forage deer (Kammermeyer and Thackston 1995; Tranel et al. 2007). Food at bait and supplemental feed sites can be consumed quickly, whereas food plots are available longer resulting in longer but less condensed exposure times to deposited prions. Deer may not shift home ranges due to presence of food plots like they might shift core use areas for a bait site, but they concentrate use of their home ranges closest to baited sites (Vanderhoof and Jacobson 1993). Food plots are often replanted annually (Harper 2019), influencing deer behavior and accumulation of prions as they are available longer on the landscape than bait.

Transects were utilized as the control treatment in this study. Waste grain congregates foraging wildlife (Nixon et al. 1991; Galle et al. 2009), and most interactions observed occurred in agricultural fields at a time when deer were actively feeding. For all three treatments, I only sampled deer during winter, but grouping behavior, movements and habitat use vary seasonally (Nixon et al. 1991). Future research should include direct observations of behavior for direct and indirect transmission throughout the year, particularly during parturition, to better understand how contact rates vary.

During both years, I recorded deer more frequently at food plots and baits sites in evening compared to morning. Beier and McCullough (1990) documented a similar increase in evening deer activity in George Reserve, Michigan, but others have reported equivalent morning and evening activity by deer (Kammermeyer and Marchinton 1977; Webb et al. 2010). However, these studies did not record deer activity at baited sites which could influence time of activity. Deer can become conditioned to feeding when bait is placed during specific times of day (Henke

1997) and because I baited deer after the peak of morning activity, it is likely that deer became accustomed to visiting sites in evening when bait was present.

I consistently observed more direct contacts between deer in 2021 than 2022, and because deer activity is influenced by winter weather (Beier and McCullough 1990; McCoy et al. 2011), I explored differences in temperature, precipitation, and snowfall between years. Temperatures ranging from 11.2-20.0 °C can increase metabolic rates and thermoregulatory costs (Moen 1985; Jensen et al. 1999), and increased snow depth can affect white-tailed deer body condition (Garroway and Broders 2005). Foraging becomes difficult as deer expend energy to scrape through snow to underlying food (Ayotte et al. 2020). Average temperatures were similar between both years of this study, but a slight decrease in precipitation was observed in 2021. An increase in snowfall was noted in February for 2021 and 2022 (+67 and 83%) compared to the 20-year average (NOAA 2023). Based on this information, I determined that weather did not have an impact on differences in direct contacts between years. I also concluded that direct and self-contacts increased as Julian date increased. This could be attributed to deer being less active during February and March (Beier and McCullough 1990), and more active during spring green-up as nutritional requirements in spring increase for deer (Ozoga 1972). The increase in self-contacts with an increase in Julian date may also correlate with deer shedding their winter coats, as I often observed large quantities of deer hair at bait sites and food plots in late March and throughout April.

Group organization in cervids is based on strong social bonds among related females and their offspring of the year while adult males segregate from females forming loosely associated bachelor groups during most of the year (Hirth 1977; Weckerly 1999; Nixon et al. 1991). Within matriarchal groups, hierarchies among related and unrelated females are developed through

relatively stable home-ranges and successfully producing female offspring who establish adjacent home-ranges to their dam (Hawkins and Klimstra 1970; Hirth 1977; Mathews and Porter 1993). Adult males dominate all other sex and age classes of deer, antlered yearling males dominate all other sex and age classes except adult males, adult females dominate yearling females and fawns, yearling females dominate fawns, and male fawns dominate female fawns (Hirth 1977; Ozoga 1972). Additionally, dominance plays an important role among groups of deer occupying similar areas; however, the probability of CWD transmission within groups of related individuals is higher than between groups of unrelated individuals (Gear et al. 2010; Storm et al. 2013).

Given deer social organization, as baiting congregates deer unnaturally in a confined area (Rustand 2010; Cosgrove et al. 2018), I expected an increase in intra- and interspecific group contacts. I also expected that deer behavior would vary among sex/age deer at different food sources. My results indicate that a direct contact was less likely to occur between adult females as the number of adult females present at a bait site increased. Adult females associate with their offspring less as their offspring advance in age, but females ≥ 3 years old still associated with their mothers 27% of the time in winter in Illinois (Nixon et al. 2010). Annual survival of adult females was high in the study area (0.746; J. Trudeau, MDDNR, unpublished data) and as a result, there were likely several intact, related matrilineal groups at my bait sites decreasing the likelihood of adult females interacting aggressively. Reduced interactions among adult females at bait sites likely lessens the risk of direct pathogen transmission. However, the likelihood of an adult male directly contacting a male fawn at a bait site increased as the number of male fawns increased. This increase in contact between adult and fawn males could be attributed to adult males needing to restore body condition after the breeding season (Nixon et al. 1994) and male

fawns needing to increase body weight to increase lifetime breeding success (Mysterud et al. 2004; Newbolt et al. 2017). This is of particular interest as adult males have a higher prevalence rate of CWD (Gear et al. 2006) and have an average dispersal distance of 9.55 km in Michigan (Pusateri 2003). Thus, adult males have increased potential to transmit prions across a greater spatial extent. As female fawn presence increased at a site, the likelihood of a direct contact with male fawns and adult females also increased. This can most likely be attributed to adult females grooming their female fawn offspring, and male fawns dominating female fawns over bait.

In Michigan, many hunters construct permanent deer blinds, concentrating bait sites and food plots to attract deer at the same location annually. This could lead to bioaccumulation of feces, urine, and saliva at the site, and thus an accumulation of prions. A common environmental contact observed was deer scraping the ground in search of food and this behavior was almost always followed by nose-to-ground behavior. These types of environmental contacts occurred more frequently at bait sites compared to food plots and transects, and these combined activities could lead to tillage of topsoil, potentially exposing buried prions and influencing indirect prion transmission. As prions are shed into the environment and bind to soil, there is a chance of prion uptake via soil ingestion. One study found that white-tailed deer, mule deer, elk, and moose regularly ingested small amounts of soil (<2% of scat samples; Beyer et al. 1994); however, despite ambiguity in the amount of exposure to infective prions needed to infect deer, this ingestion of soil could still be an indirect risk to contacting CWD. Wildlife agencies can help reduce or slow the spread of disease by implementing and enforcing baiting bans (Rudolph 2012; Cosgrove et al. 2018). However, when a baiting ban was implemented in Michigan to prevent the spread of bovine tuberculosis, there was a non-compliance rate of ~25% in the immediate area (Rudolph 2012). Changing hunter behavior to cease the use of bait as a hunting tool can only be

achieved through educational awareness of associated penalties and applying penalties that hunters consider significant, such as loss of hunting privileges (Rudolph 2012).

Scraping and nose-to-ground behavior also could have implications for self-contact behaviors as a potential route of prion transmission. For example, as deer scrape the ground with their hooves or put their nose to the ground, prions could adhere to their hooves or nose. Two common behaviors I observed were deer scratching their body with their hooves and self-grooming. If prions were present on the hooves or nose after scraping or nosing the ground, and then they scratch their body, prions could be deposited on the body and then they could groom the same spot. There is a risk of prion transmission in this event, however, I believe risk of transmission is minor through this pathway because the potential for ingestion seems less likely compared to the amount that might be ingested from direct contact with an infected individual or indirectly through infected environmental materials. The same can be said for an individual that scraped the ground or nosed the ground, and then grooms, nuzzles, or kicks another individual. There are many potential routes of pathogen transmission to observe, but the level of risk with each route may vary greatly. Risk of pathogen transmission increases over time the longer that feed sites are maintained and deer are exposed (Thompson et al. 2008; Murray et al. 2016; Mejia-Salazar et al. 2018).

This study is limited by not knowing familial relationships of interacting individuals. However, I could make reasonable assumptions under certain circumstances. For example, if only a single doe and fawn were present, they would likely be related (Nixon et al. 1991, 2010). It would be beneficial to address relatedness by radio-collaring or marking individuals and using DNA to establish matrilineal lines in an area. Investigating cross-species contact at supplemental

feed sites would also provide additional information for pathogen transmission risk across species barriers (Bowman et al. 2015).

Additional Behavioral Observations

While observing deer at bait sites, food plots, and in the surrounding landscape, I noted behaviors not analyzed for this thesis including aggressive non-contact behaviors (stomping, rising up, posturing, and chasing). Anecdotally, it appeared adult males displayed the most aggressive non-contact behaviors compared to other sex-age groups at bait sites. This could be attributed to food competition to replenish body condition post-rut (Nixon et al. 1994; Clutton-Brock et al. 1982). Alternatively, as adult males in the study area have a survival probability of 0.57 during the hunting season (J. Trudeau, MDDNR, unpublished data), aggressive behaviors could be related to establishing dominance as dominant mature adult males are removed from the population (Nixon et al. 1991, 1994).

Deer of all sex-age groups were often observed smelling or rubbing their noses, sometimes licking the PVC posts at the center of the bait site or food plots. It happened most often at bait sites, and this behavior did not seem to occur as much with t-posts that marked the outer perimeter of the site. A marked doe from a previous study was present at one bait site from January-April 2022; she was the matriarch of her family group and would aggressively contact other adult females and fawns in the baited area if they did not leave. This marked adult female had a female fawn, who over the duration of the field season became increasingly aggressive herself. I suspect she was displaying dominance because of her mother's dominance in the herd. Deer of all sex-age classes were observed exhibiting "aggressive non-contact" behaviors including stomping their front hoof, rising up on their back legs, chasing other individuals, and posturing. These behaviors were a precursor, serving as a warning, before true aggressive contact behaviors occurred. Hirth (1977) described many of these behaviors in detail and ordered them relative to increasing aggression that ultimately led to direct contact.

Anecdotally, I observed deer checking bait sites regularly after bait was depleted for several days between site visits. In a model utilizing GPS-collar data, researchers showed that mule deer migrations are based on spatial memory passed on from generations and experience rather than behavioral decisions to optimize local foraging (Merkle et al. 2019). If a site used to feed deer is at the same location annually, prolongs the feeding period, and the frequency of use remains high, deer may learn the location and continue to visit across generations. Within this confined space, high concentrations of saliva, urine, and feces could be deposited. Concentration of feces and bodily fluids could result in a buildup of prions in the area if infected animals are present as prions are known to persist in the environment by binding to soil and plants (Pritzkow et al. 2015; Kuznetsova et al. 2020). A localized buildup of prions could create a disease “hotspot”.

Lastly, Garner (2001) observed deer using the heat from their breath to thaw frozen bait for consumption which has implications for pathogen transmission. This was not something I witnessed, but if food was frozen to the ground, I often observed deer scraping the ground with their front hooves at bait sites, food plots, and the surrounding landscape. In some circumstances, they were trying to access food underneath the snow and other times they were trying to unearth corn that may have been covered due to rainfall or deer activity turning it under the ground. Either way, it was rare to re-bait a site and observe even a few kernels of corn remaining.

Chapter Two Tables

Table 2.1 Number of deer-triggered videos recorded at bait sites and food plots during winter (January through April) in Michigan, USA, 2021 and 2022. The morning survey period occurred 15 minutes before sunrise and ended 2 hours after sunrise. The evening survey period began 2 hours before sunset and ended at most 15 minutes after sunset.

Treatment	Survey period	Year	Total 2-min videos
Bait site	Morning	2021	813
		2022	2,815
	Evening	2021	1,783
		2022	7,287
Food plot	Morning	2021	115
		2022	354
	Evening	2021	369
		2022	1,125

Table 2.2 Sex-age class of deer observed in 30-second segments along transects and at bait sites and food plots during winter (January through April) in Michigan, USA, 2021-22.

Treatment	Sex-age group	Number of deer observations		30- second segments	
		2021	2022	2021	2022
Transects (n=35)	Adult male	12	86	40	111
	Adult female	56	74	197	102
	Male fawn	24	57	81	74
	Female fawn	39	47	135	61
	TOTAL	131	264	453	348
Bait Sites (n=20)	Adult male	201	298	672	966
	Adult female	61	355	175	1,129
	Male fawn	94	361	293	1,193
	Female fawn	36	225	114	709
	TOTAL	392	1,239	1,254	3,997
Food Plots (n=19)	Adult male	57	48	158	115
	Adult female	42	74	129	181
	Male fawn	32	85	82	220
	Female fawn	11	67	24	149
	TOTAL	142	274	393	665

Table 2.3 Total number of direct, self, or environmental contacts exhibited by deer sex-age class by treatment during winter (January through April) in Michigan, USA, 2021-22. Note that multiple behavior types could occur within one 30-second segment.

Deer Sex-Age Group	Total deer observations by year		Contact Type by Year					
			Direct		Self		Environmental	
	2021	2022	2021	2022	2021	2022	2021	2022
Transects								
Adult Male	12	86	4	19	2	22	30	96
Adult Female	56	74	4	11	14	11	143	75
Male Fawn	24	57	6	11	7	16	65	67
Female Fawn	39	47	4	9	11	11	110	48
Total	131	264	18	50	34	60	348	286
Bait Sites								
Adult Male	201	298	132	92	26	59	646	874
Adult Female	61	355	54	172	15	92	161	967
Male Fawn	94	361	65	151	12	94	282	1,118
Female Fawn	36	225	27	120	8	67	106	631
Total	392	1,239	278	535	61	312	1,195	3,590
Food Plots								
Adult Male	57	48	22	3	5	3	143	97
Adult Female	42	74	28	8	4	5	118	154
Male Fawn	32	85	21	10	3	9	76	200
Female Fawn	11	67	2	6	0	5	22	129
Total	142	274	73	27	12	22	359	580

Chapter Two Figures

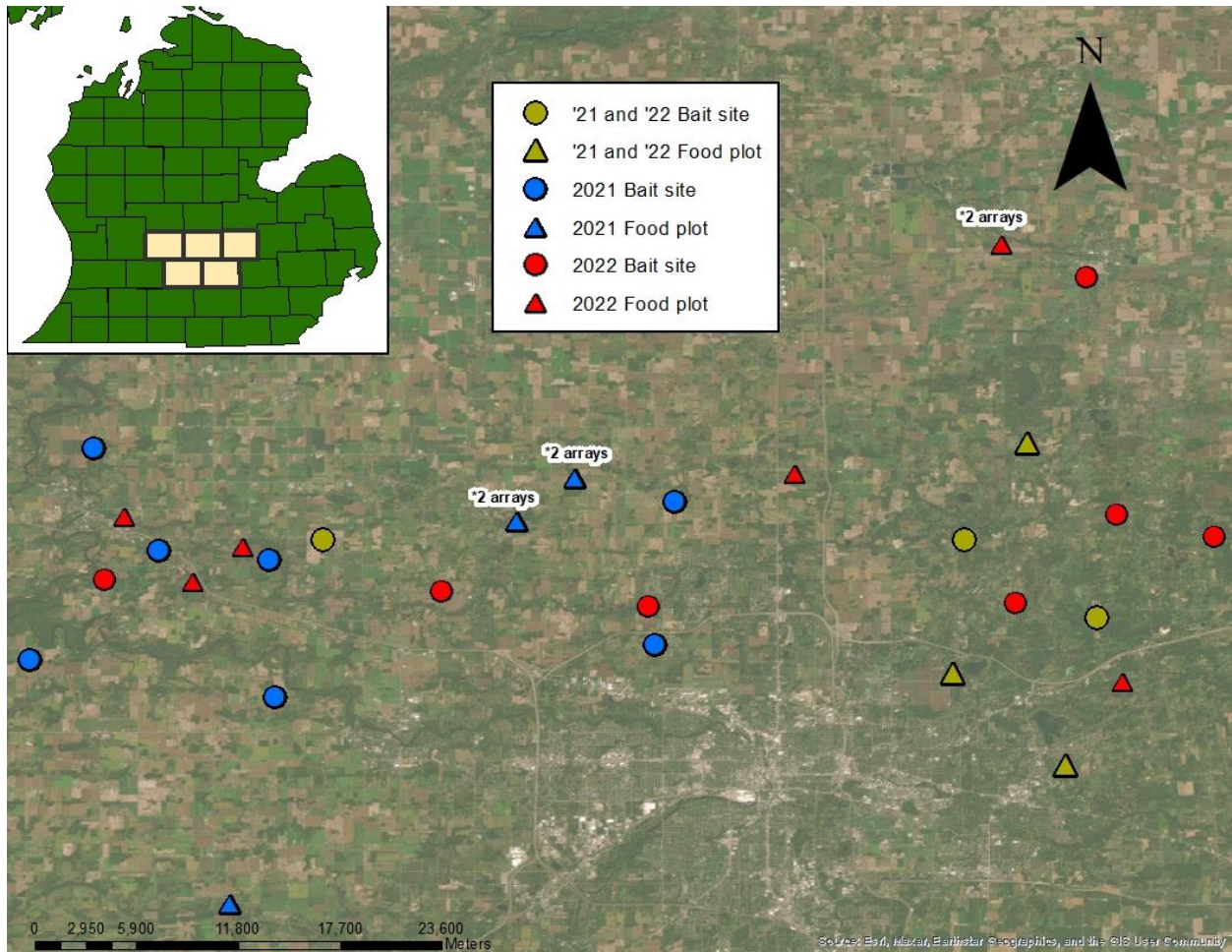


Figure 2.1 Locations of bait site and food plot camera arrays to record deer behaviors during winter (January through April) in Michigan, USA, 2021-22. Background is World Imagery layer updated in 2023 by Esri, Maxar, Earthstar Geographics and the GIS User Community.

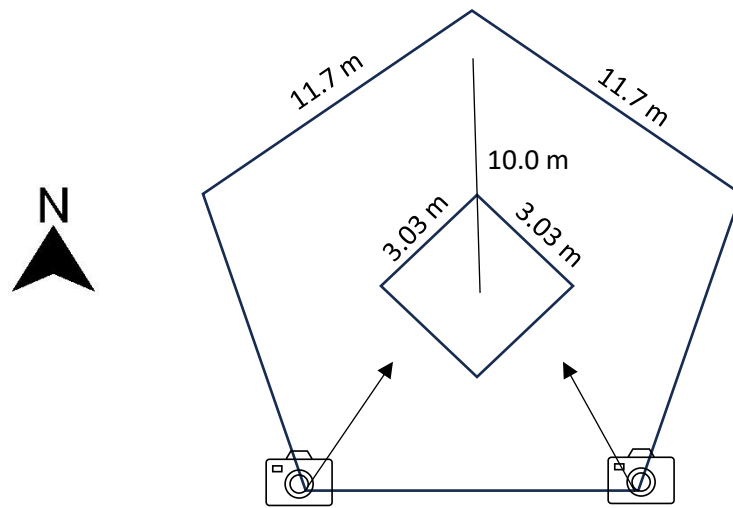


Figure 2.2 Configuration of bait site and food plot camera arrays to record deer use and behaviors during winter (January through April) in Michigan, USA, 2021-22. T-posts demarcated corners of the pentagon, and PVC pipe the inner square. Corn (7.5 L) was spread in the inner square. Motion-triggered cameras were placed on the south t-posts facing towards the bait area.

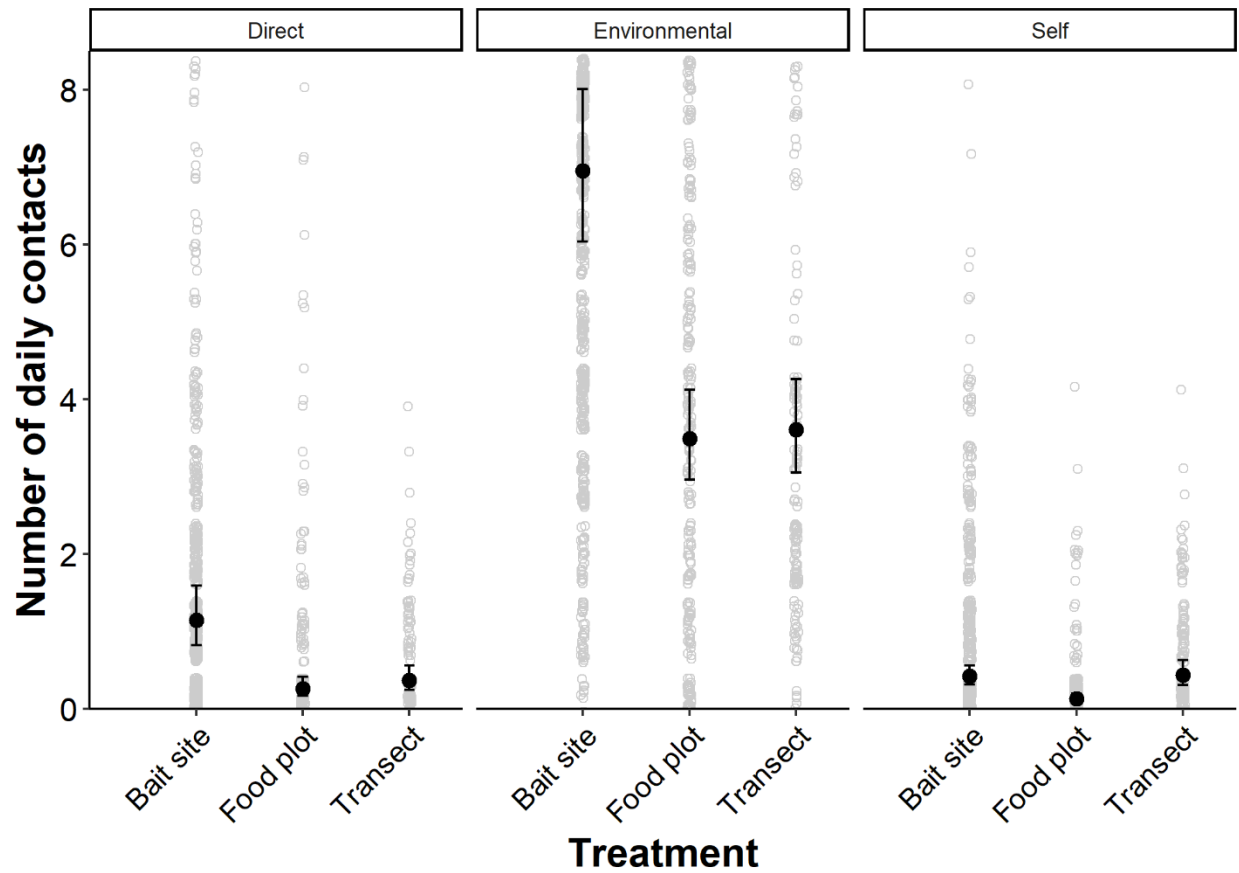


Figure 2.3 Average number of daily direct, environmental, and self-contacts among deer observed at bait sites, food plots, and transects during winter (January through April) in Michigan, USA, 2021-22. Light grey circles represent data points, and error bars represent 95% confidence intervals.

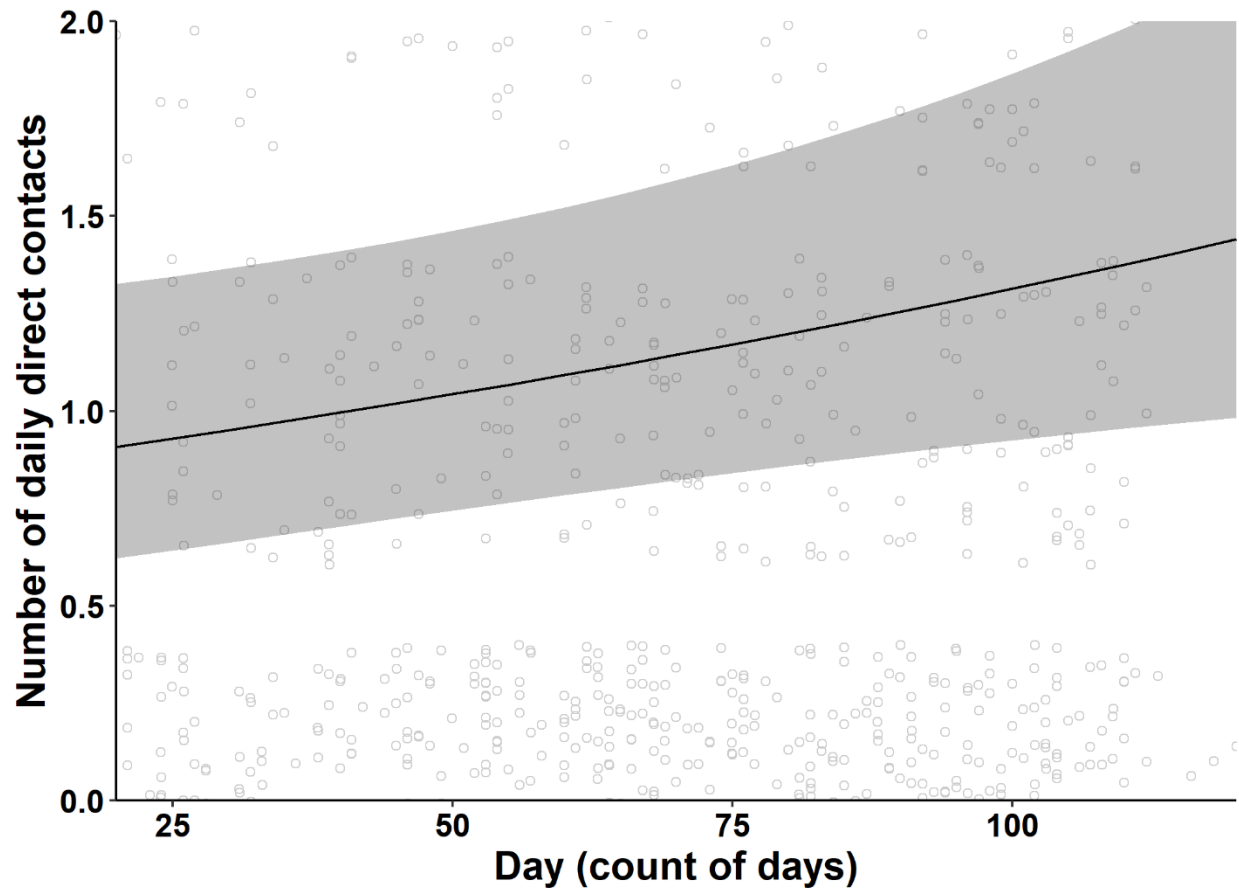


Figure 2.4 Estimated number of direct contacts by day starting on January 4th thru April 25th among deer at bait sites, food plots, and transects in Michigan, USA, 2021-22. Light grey circles represent data points, and grey shading represents 95% confidence intervals.

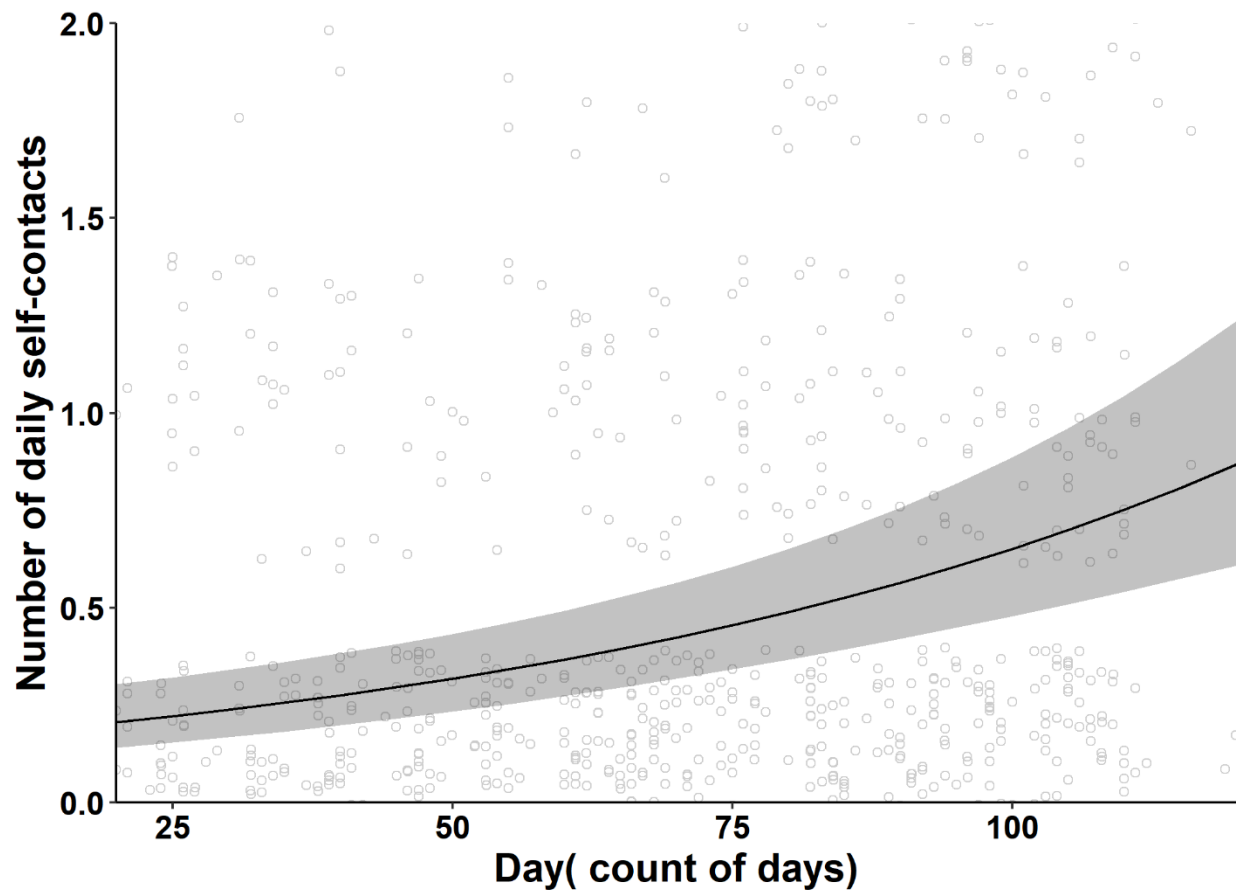


Figure 2.5 Estimated number of self-contacts by day starting on January 4th thru April 25th among deer at bait sites, food plots, and transects in Michigan, USA, 2021-22. Light grey circles represent data points, and grey shading represents 95% confidence intervals.

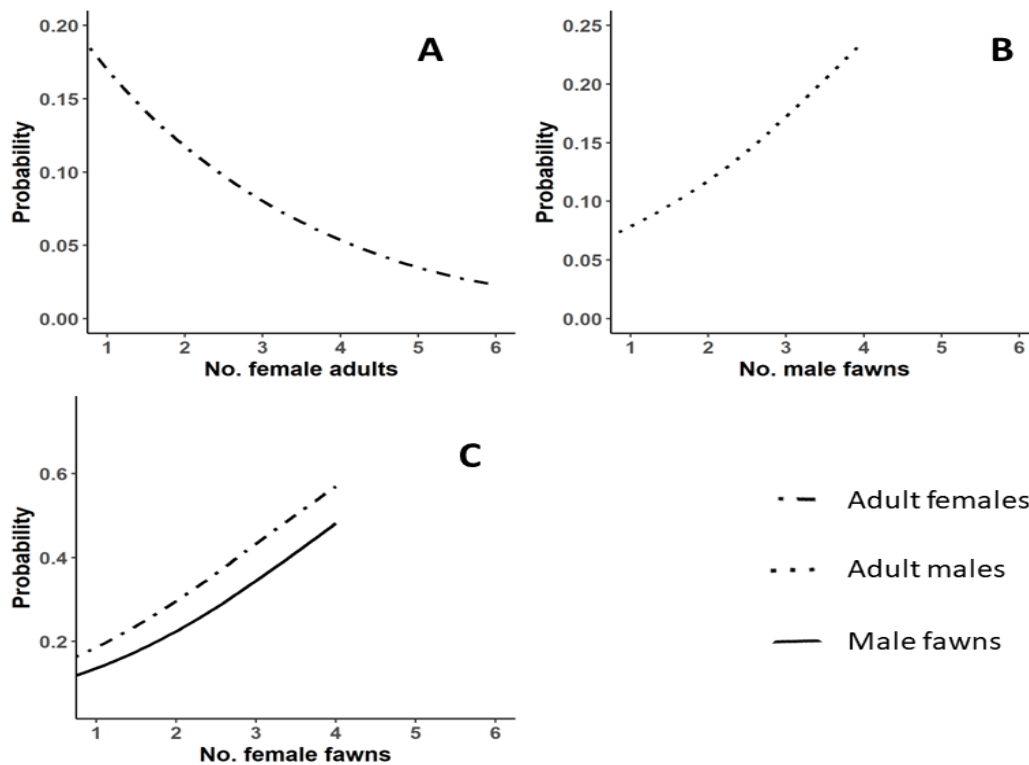


Figure 2.6 Probability of direct contact occurring between conspecifics at bait sites during winter (January through April) in Michigan, USA, 2021-22. A = graph in upper left depicting the probability of an adult female directly contacting other adult females as the number of adult females at a bait site increases, B = graph in the upper right showing the likelihood of an adult male directly contacting a male fawn as the number of male fawns increases, C = graph in the bottom left showing the probability adult females and male fawns contacting female fawns as the number of female fawns increases at a bait site.

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APPENDIX II: TABLES

Table A.2.1 Categories (bold-faced) and descriptions of deer behaviors observed in Michigan, USA, 2021-22.

Name	Description
<i>Direct contact</i>	
Push	Pushing another deer with head or body
Bump	Contacts another deer with nose on any portion of body except the face
Flail ^{ab}	Rising on hind legs and striking another deer using a paddle motion
Strike ^{ab}	Includes rising on hind legs and contacting another deer with front legs or kicking another deer with front or hind foot
Head-to-head ^a	Two deer rub or push their heads together, includes sparring- may or may not be aggressive
Groom-other ^a	Lick another deer
Nuzzle ^a	Using muzzle to rub the nose or face of another deer
<i>Self-contact</i>	
Self-groom	Deer licks itself
Body scratch	Hoof contacts body
Head scratch	Hoof contacts head
<i>Environmental Contact</i>	
Scrape	Scraping ground with hoof
Nose-to-ground	Feeding or not
Browse	Eat/chew on wood vegetation or other objects
Roll	Rolls on ground

^a Hirth 1977.

^b Thomas et al 1965.

Table A.2.2 Parameter estimates from a negative binomial mixed model of direct contacts in deer across treatments during winter (January through April) in Michigan, USA, 2021-22. Bait sites served as the reference level in estimating treatment effects and is labeled as intercept in the table. SE = standard error; CI = confidence intervals.

Parameter	Estimate(SE)	Lower 95% CI	Upper 95% CI
Intercept (Bait Site)	0.13 (0.16)	-0.19	0.46
Food Plot	-1.45 (0.27)	-2.00	-0.90
Transect	-1.12 (0.26)	-1.64	-0.59
Date	0.12 (0.05)	0.02	0.21

Table A.2.3 Parameter estimates from a negative binomial mixed model of self-contacts in deer across treatments during winter (January through April) in Michigan, USA, 2021-22. Bait sites served as the reference level in estimating treatment effects and is labeled as intercept in the table below. SE = standard error; CI = confidence intervals.

Parameter	Estimate(SE)	Lower 95% CI	Upper 95% CI
Intercept (Bait Site)	-0.85 (0.14)	-1.14	-0.57
Food Plot	-1.14 (0.25)	-1.64	-0.64
Transect	0.04 (0.22)	-0.39	0.48
Date	0.37 (0.06)	0.25	0.49

Table A.2.4 Parameter estimates from a negative binomial mixed model of environmental contacts in deer across treatments during winter (January through April) in Michigan, USA, 2021-22. Bait sites served as the reference level in estimating treatment effects and is labeled as intercept in the table below. SE = standard error; CI = confidence intervals.

Parameter	Estimate (SE)	Lower 95% CI	Upper 95% CI
Intercept (Bait Site)	1.93 (0.07)	1.79	2.08
Food Plot	-0.68 (0.10)	-0.90	-0.47
Transect	-0.65 (0.11)	-0.87	-0.43
Date	0.02 (0.02)	-0.02	0.06

Table A.2.5 Parameter estimates for a generalized linear mixed effects model using Penalized Quasi-Likelihood evaluating likelihood of a direct contact exhibited by an adult male deer relative to conspecifics, year, and Julian date at bait sites during winter (January through April) in Michigan, USA, 2021-22. SE = standard error; CI = confidence interval.

Parameter	Estimate (SE)	Lower 95% CI	Upper 95% CI
Intercept	-3.24 (0.49)	-4.21	-2.27
Adult male	0.02 (0.12)	-0.22	0.27
Adult female	0.09 (0.22)	-0.34	0.53
Male fawn	0.45 (0.13)	0.19	0.71
Female fawn	-0.02 (0.42)	-0.86	0.81
Year (2022)	-0.88 (0.24)	-1.37	-0.39
Julian date	0.009 (0.005)	-0.001	0.02

Table A.2.6 Parameter estimates for a generalized linear mixed effects model using Penalized Quasi-Likelihood evaluating likelihood of a direct contact exhibited by an adult female deer relative to conspecifics, year, and Julian date at bait sites during winter (January through April) in Michigan, USA, 2021-22. SE = standard error; CI = confidence interval.

Parameter	Estimate (SE)	Lower 95% CI	Upper 95% CI
Intercept	-1.84 (0.58)	-2.99	-0.68
Adult male	0.24 (0.98)	-1.68	2.17
Adult female	-0.43 (0.17)	-0.78	-0.09
Male fawn	0.32 (0.17)	-0.02	0.66
Female fawn	0.65 (0.20)	0.25	1.05
Year (2022)	-1.31 (0.37)	-2.05	-0.57
Julian date	0.009 (0.005)	-0.0003	0.01

Table A.2.7 Parameter estimates for a generalized linear mixed effects model using Penalized Quasi-Likelihood evaluating likelihood of a direct contact exhibited by a male fawn deer relative to conspecifics, year, and Julian date at bait sites during winter (January through April) in Michigan, USA, 2021-22. SE = standard error; CI = confidence interval.

Parameter	Estimate (SE)	Lower 95% CI	Upper 95% CI
Intercept	-3.31 (0.57)	-4.44	-2.17
Adult male	0.27 (0.34)	-0.39	0.95
Adult female	0.24 (0.16)	-0.06	0.56
Male fawn	0.24 (0.19)	-0.14	0.63
Female fawn	0.62 (0.26)	0.10	1.13
Year (2022)	-0.83 (0.32)	-1.47	-0.19
Julian date	0.0003 (0.004)	0.001	0.01

APPENDIX II: FIGURES

DHARMa residual

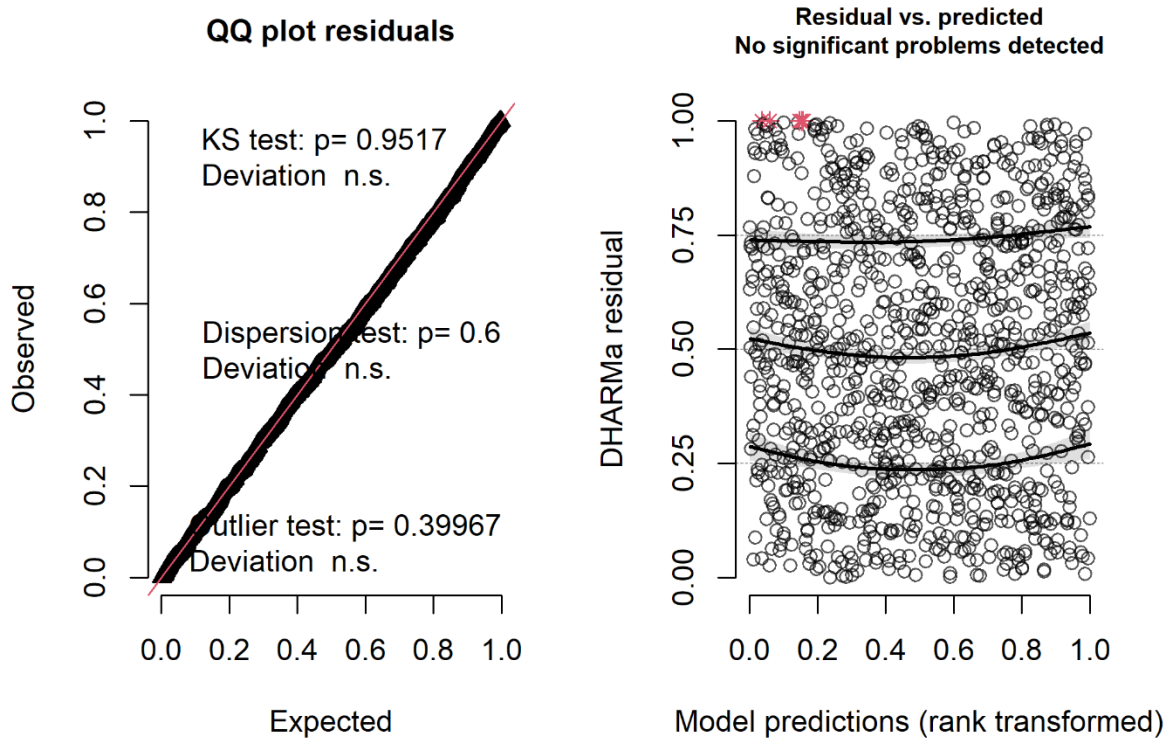


Figure. A.2.9 A quartile-quartile (QQ) plot of the direct contact behavior model residuals (left panel) showing observed values on the y-axis and expected values on the x-axis. Residual plot (right panel) showing residual values on the y-axis and predicted model values on the x-axis. Empirical 0.25, 0.5, and 0.75 quantiles depicted by the solid red line (left panel) are compared to theoretical 0.25, 0.5, and 0.75 quantiles depicted by black lines (right panel) Red stars in the indicate potential outliers.

DHARMA residual

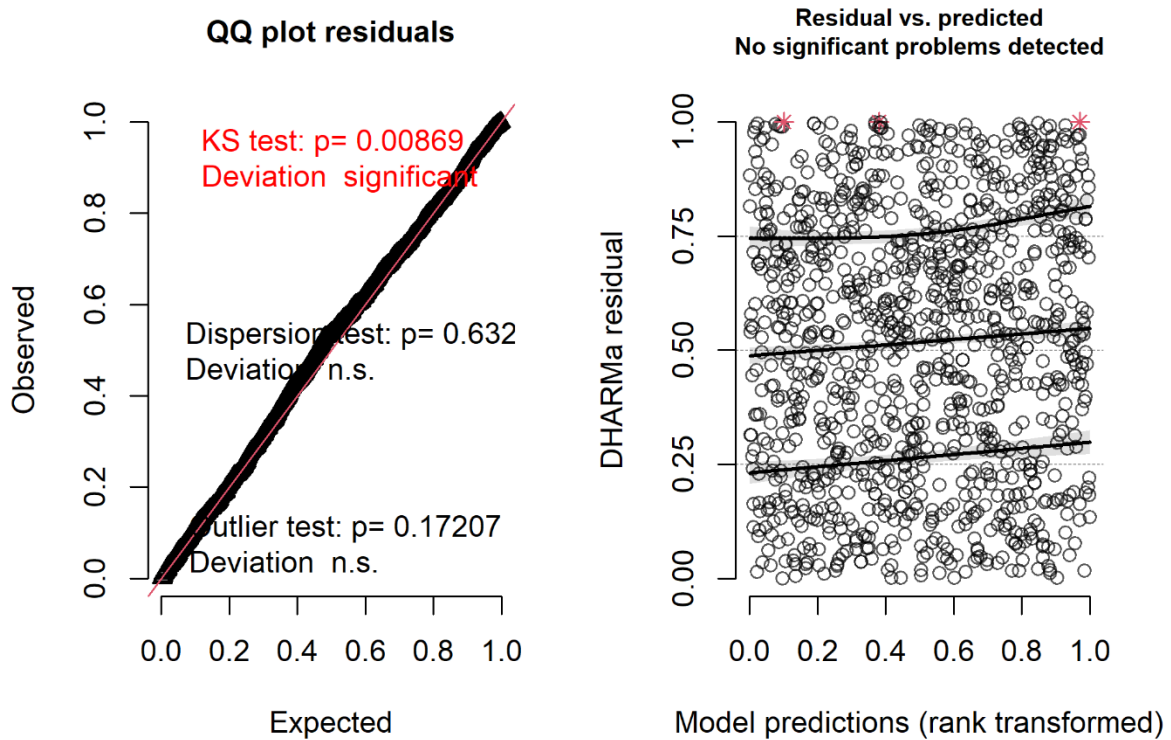


Figure. A.2.10 A quartile-quartile (QQ) plot of the self-contact behavior model residuals (left panel) showing observed values on the y-axis and expected values on the x-axis. Residual plot (right panel) showing residual values on the y-axis and predicted model values on the x-axis. Empirical 0.25, 0.5, and 0.75 quantiles depicted by the solid red line (left panel) are compared to theoretical 0.25, 0.5, and 0.75 quantiles depicted by black lines (right panel) Red stars in the indicate potential outliers.

DHARMA residual

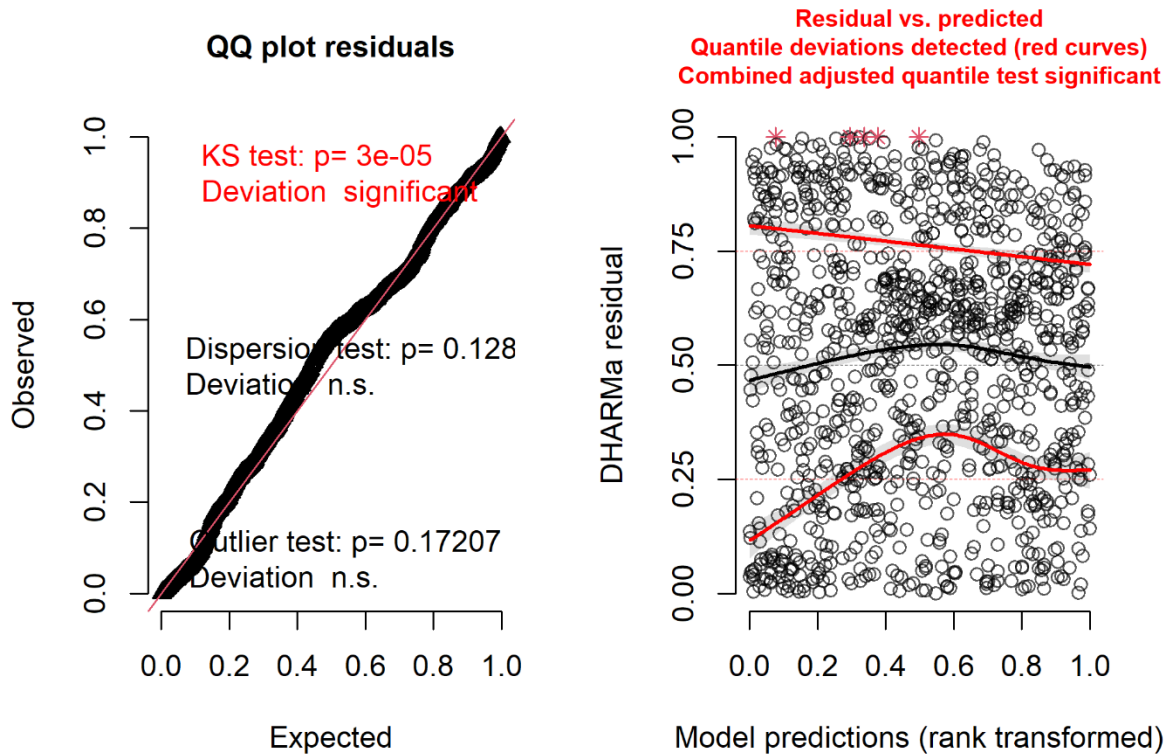


Figure. A.2.11 A quartile-quartile (QQ) plot of the environmental contact behavior model residuals (left panel) showing observed values on the y-axis and expected values on the x-axis. Residual plot (right panel) showing residual values on the y-axis and predicted model values on the x-axis. Empirical 0.25, 0.5, and 0.75 quantiles depicted by the solid red line (left panel) are compared to theoretical 0.25, 0.5, and 0.75 quantiles depicted by black lines (right panel) Red stars in the indicate potential outlier.

CONCLUSION

As CWD continues to spread across the United States, wild populations of cervids are threatened. Deer, elk, and moose populations are all at risk of population decline and state and federal agencies allocate significant funding to CWD research, prevention, surveillance, and control once it is established in an area. The allocation of this funding coupled with the potential decrease in Pittman-Robertson funds from reduced hunter participation could result in a significant impact in overall conservation funding. Ongoing research may help fill in knowledge gaps that are critical to the management of CWD.

Understanding how deer utilize landscapes can help agencies identify potential “hotspot” areas and employ localized management practices. Few studies have tried to quantify the landscape variables that influence where deer congregate during the winter in agriculturally dominated areas and how this may influence group size. Additionally, epidemiological models use a suite of variables to predict how CWD may spread across a landscape. However, some of these variables, such as direct and indirect contact rates among deer, are estimated using GPS-collar and proximity logger data that is not precise and does not account for contacts among uncollared individuals. Evaluating contact rates on the dominant landscape is important for models, but also understanding how deer interact at food plots and bait sites is important for the hunting community, the main group funding natural resource conservation.

To address these knowledge gaps, I used road-based surveys and trail cameras across a five-county area of southern Michigan to evaluate congregation areas and contact rates from January-April 2021 and 2022. I ran 35 – 4.83 km long transects several times per week. I recorded information regarding group demographics, location, and behavior of select individuals. Using USDA-CDL in ArcMap, I evaluated dominant cover and crop types in a 740 m radii buffer

around each recorded group location. I used a GLMM to predict the effects of landscape variables on observed deer group sizes. I investigated deer contact rates by establishing trail cameras at bait sites and food plots on privately-owned land. I quantified exhibited behaviors across sex-age classes and used a GLMM to predict the likelihood of a behavior category and included date and treatment type (bait site or food plot) as predictor variables. I also evaluated the likelihood of direct contact occurring among conspecifics at bait sites.

I found that deer group size ranged from 1 - 67 individuals. Group sizes increased by ~1.5 – 3.0 deer as total hectares of corn and forage crop increased. As distance from the nearest building increased, so did group size. I found that residential and forest cover types had a negative impact on group size, and a positive impact associated with agricultural cover types. Contagion had a lower, but significant impact on group size, with larger, homogenous land cover corresponding to lower group sizes.

I compiled 395 observations of known sex-age deer during road-based surveys and conducted 2,047 observations from video surveys (bait sites = 1,631, food plots = 416). Direct contacts occurred most frequently at bait sites, followed by food plots, and lastly the surrounding landscape. Self-contacts occurred less often at food plots compared to bait sites, but there was no difference between bait sites and the surrounding landscape. Both direct and self-contacts increased as Julian date increased. Environmental contacts were observed most often at bait sites. At bait sites, adult males were more likely to exhibit a direct contact when in proximity to more male fawns. Adult females were less likely to directly contact each other when the number of adult females increased. The likelihood of a direct contact occurring between a male or female fawn with an adult female increased as the number of adult females at a bait site increased.

These findings can fill knowledge gaps to help improve epidemiological models and assist wildlife agencies with identifying potential localized “hotspots”. As deer congregate in winter and group sizes get larger, there is an inherent increase in prion deposition and uptake. By understanding the features of the landscape that these larger groups select for, wildlife agencies can allocate resources in a more targeted manner to help prevent or slow the spread of disease. Working with local farmers to alter farming practices to address areas of congregation or potentially in the future spread fields with prion deactivating treatments could help mitigate disease. Culling success could increase by targeting larger corn and forage crop fields adjacent to woodlots and >222m away from any buildings. My findings confirm that during winter direct contacts do not happen often at bait sites, food plots, or on the surrounding landscape; however, baiting does increase direct contact, thus increasing the probability of disease transmission. As environmental contacts happened the most often at any setting, I believe this route of transmission needs additional exploration. Overall, the results from my study provide models with more accurate contact rates among sex-age groups during a critical period of congregation and aid wildlife agencies with knowledge to employ efficacious techniques to manage disease.

While this study may have filled some knowledge gaps, it has brought forward additional questions. By marking individuals and utilizing similar methodology, we can better understand the interactions and contact rates among mixed family groups at bait sites and food plots. This research was conducted only during the winter, which only sheds light upon contact rates at one time of year. Direct observations for the remaining three seasons would greatly benefit epidemiological models that utilize contact rates. My results indicated that environmental contacts occurred frequently. Additional research should focus on the frequency of these behaviors year-round and test for prions on environmental objects, such as licking branches or

scrapes. Additional sampling for prions should occur in common congregation areas like corn fields adjacent to woodlots. The lack of inquiry into treatment of farm fields for infected prions warrants additional research to help combat CWD on the landscape long-term after a population has been culled.