



## INVESTIGATION OF MOVEMENT DYNAMICS OF WILD DEER IN SOUTHEASTERN MINNESOTA TO UNDERSTAND POTENTIAL SPREAD OF CHRONIC WASTING DISEASE

Chris Jennelle, Joanne Crawford, and Michelle Carstensen

### SUMMARY OF FINDINGS

The Minnesota Department of Natural Resources (MNDNR) is in the third year of a continuing study to investigate the movement dynamics of wild white-tailed deer (*Odocoileus virginianus*) in southeastern Minnesota. This project evolved after the detection of chronic wasting disease (CWD) in fall 2016 in Fillmore County and is designed to 1) understand potential pathways of CWD spread on the landscape by movement of wild deer, 2) increase our likelihood of managing the outbreak in this and other areas of Minnesota, and 3) estimate general causes of deer mortality in southeastern Minnesota. In mid-February 2020, we captured and fitted GPS collars to 56 white-tailed deer fawns (31 females, 25 males) in a study area of approximately 2,000 square miles centered on Preston, MN. We collared a total of 226 deer since the study began in March 2018 and as of June 2020, continue to monitor 74 animals that remain available for tracking. There have been 82 known mortalities due to hunter-harvest (n=36), vehicle collision (n=12), capture-related issues (n=12), underlying health conditions (n=6), indeterminate causes (n=6), agency culling (n=4), trauma (n=4), and predation/scavenging (n=2). Average annual survival for females and males was 0.73 (CI: 0.62-0.86) and 0.54 (CI: 0.40-0.73), respectively, and the difference was marginally significant ( $Z=1.80$ ;  $P=0.072$ ). Average annual mortality due to hunter harvest was 18%, while that for other causes and vehicle collision were 11% and 6%, respectively. The low survival estimates reflect liberalized harvest regulations within the study area in order to manage CWD, coupled with the fact that yearlings and young adults are the most vulnerable group to hunter harvest. Overall, a large number of deer were censored due to collar failures; however, the failure rate has improved from 90 collar malfunctions in 2018, to 17 in 2019, and 2 in 2020. We averaged segment-derived home ranges across seasons for 127 deer (62 females, 65 males) from 2018-2019; average 50% core area size was 0.35 km<sup>2</sup> (CI: 0.28-0.42) and 0.50 km<sup>2</sup> (CI: 0.39-0.62) for females and males, respectively. Average 95% home range size was 1.75 km<sup>2</sup> (CI: 1.37-2.13) and 2.21 km<sup>2</sup> (CI: 1.72-2.70) for females and males, respectively. We found that 26% of females and 43% of males dispersed between their natal and adult home range, and this difference was marginally significant ( $\chi^2=2.73$ ,  $P=0.10$ ). Surprisingly we found that 15% of females and 6% of males underwent apparent seasonal migration between summer and winter ranges, although there was no significant difference between these proportions ( $\chi^2=1.70$ ,  $P=0.19$ ). The average distance traveled for females and male dispersers was 20.0 km (CI: 5.67-30.10) and 22.8 km (CI: 11.70-32.30), respectively. The average distance traveled for migratory females and males was 12.8 km (CI: 3.49-18.40) and 17.7 km (CI: 1.35-27.20), respectively. We observed more extreme dispersal distances by both sexes, with the maximum linear distance traveled by a female and male of 116 km and 97 km, respectively. Many animals in the study conducted temporary excursions from their home range, lasting hours to several days. We are currently in the process of analyzing these types of movements to find any patterns that might emerge. Taken together, these results underscore the high degree of deer movement by both sexes across the southeastern Minnesota landscape and potential for yearlings in particular to facilitate spatial spread of CWD. Furthermore, at least for yearling and young adult deer (2.5-3.5

years old) in this region of Minnesota, hunting appears to be the dominant cause of mortality. This underscores the importance of harvest management as a valuable tool to control and suppress CWD spread and magnitude in southeastern Minnesota.

## INTRODUCTION

Chronic wasting disease (CWD) is a fatal infectious disease first characterized in the late 1960s in Colorado that affects elk (*Cervus canadensis*), mule deer (*O. hemionus*), white-tailed deer, reindeer (*Rangifer tarandus*) and moose (*Alces alces*). It has been detected in wild and captive cervids in 26 states and 3 Canadian provinces in North America, as well as Finland, Norway, South Korea, and Sweden. Work has demonstrated that CWD can cause population declines in white-tailed deer and mule deer in the western US, particularly when high prevalence levels occur in a population (Edmunds et al. 2016, DeVivo et al. 2017). In the upper Midwestern US, an ongoing study of CWD in white-tailed deer in Wisconsin has shown that CWD-infected deer die at 3x the rate of uninfected deer (Wisconsin DNR 2018). In the same CWD system, research has shown that deer regularly die from CWD in the wild, although they typically go undetected by people (Samuel and Storm 2016).

It has been nearly 4 years since the Minnesota Department of Natural Resources (MNDNR) discovered CWD during the 2016 regular hunting season in Fillmore County, Minnesota, and through 16 June 2020, 88 wild deer have tested positive in Minnesota (including one from Pine Island in 2010). Since October 2019, there have been 35 new CWD detections in wild deer, all but one located in the southeast CWD Management Zone. With the exception of an adult buck that tested positive for CWD in Dakota County in March 2020, the pattern of new detections in Minnesota suggests that spatial spread of CWD continues to radiate from the core areas around Preston, MN and a previously positive captive cervid facility in Winona County (Figure 1). The precise mechanism(s) of CWD introduction to these areas cannot be confirmed, but potential hypotheses include natural movement of infectious deer from neighboring states (e.g., Wisconsin, Iowa, or Illinois), contact between wild deer and prior CWD-positive captive cervid facilities, or contamination of the environment with infectious cervid carcass material. Given the threat of CWD in southeastern Minnesota, this study seeks to better understand natural deer movement ecology and in particular detect seasonal corridors of movement that may inform our management of CWD spatial spread.

As infected and non-infected deer interact and move across the landscape, they transmit infectious prions through direct contact with other deer or indirectly through environmental deposition (Almberg et al. 2011). Limited information exists about deer contact rates and their relationship to transmission rates. The presumed main driver of spatial spread among wild deer are natural movements, which vary as a function of season, sex, age, habitat, underlying deer density, and other variables (Nixon et al. 2007, Long et al. 2008, Long et al. 2010, Lutz et al. 2015, Peterson et al. 2017). Besides our current study, there is only one published study on deer movement ecology in southeastern Minnesota. However, the Wisconsin Department of Natural Resources has an ongoing study in its fourth year designed to understand the impacts of CWD on survivorship and movements of deer in Wisconsin, which will be useful in providing a context for the implications of regional movements of wild deer and CWD spread.

Deer behavior and movements vary by sex, season, and landscape features, along with deer population demographics and social structure. Three types of movement likely facilitate disease spread across the landscape including dispersal events, recurrent seasonal movements, and temporary excursion events. The most substantial long-distance movements involve dispersal from natal to adult ranges, most likely to occur in 1-year-old deer during spring, although males may also disperse in fall. We define dispersal in this context as an asymmetric movement from the natal home range to a distinct and non-overlapping adult range. While dispersal usually

occurs once, there are cases of 2-stage dispersals when a deer makes a second asymmetric movement to a second adult home range, but this is rare. Recurrent seasonal movements can include migratory behavior and movements between summer and winter ranges. Excursions (or synonymously forays) are temporary transient movements out of an established home range that typically occur in fall, likely influenced by mating behaviors. Because deer densities and movement behavior can be altered by management actions, a better understanding of both deer density and movement activities related to density will enhance our ability to effectively manage disease risk in the Minnesota deer population. The importance of this research is underscored by the unabated spread of CWD both between and within states, and the need to find management solutions to suppress the spread of disease arising from natural deer movements.

## METHODS

### Study Area

The study area, approximately 7,250 km<sup>2</sup>, is centered on Preston, MN, in Fillmore County where the CWD cases in wild deer during 2016 appeared first (Figure 1). The study area limits are flexible and established as an approximately 30-mile buffer around Preston, MN, which includes much of the Southeast CWD Management Zone. We included extensive areas extending through Fillmore, Winona, Houston, and Olmsted Counties to capture and release Geographic Position System (GPS)-collared deer, so that our collared sample is representative of the yearling to young adult (2.5-3.5. year olds) deer population in southeastern Minnesota (Figure1).

Deer in southeastern Minnesota are managed within CWD Disease Management permit areas (DPA) in the 600-series, where the deer population is well above population objectives and disease management is the primary goal. Therefore, harvest regulations were liberalized in the study area with 3 seasons; Archery (Sept 14. - Dec 31), two 9-day firearms season, and a 16-day muzzleloader season. Harvest was unlimited for antlerless deer and limited to 1 legal buck per season (the 3-buck limit occurred in fall 2019 only). Additionally, 3-day youth hunts and early antlerless seasons took place in October of each year. Special late-season hunts (3-day) took place each year in select DPAs where CWD had been detected during the regular season. In 2019, the average deer harvest across the study area was about 5 deer per mi<sup>2</sup> compared to about 1.9 deer per mi<sup>2</sup> in 2016 prior to implementation of liberalized harvest regulations to control CWD.

The study area is composed of a matrix of agricultural lands interspersed with deciduous forest upon a landscape of rolling hills and in some cases very steep ridges and valleys. There is considerable heterogeneity in landscape topography and land use. The eastern part of the study area is composed of forested bluff lands and steep ridges and moving southwesterly, the landscape transitions to be flat and dominated by agriculture. More than 90% of the landscape is held in private ownership. There is significant heterogeneity in deer density due to both habitat variability and localized refugia (i.e., parcels with viable deer habitat where hunting is not permitted) with average deer density about 25.4 deer mi<sup>2</sup> (range 12-42).

Coyotes (*Canis latrans*) are the primary predators of deer in the region and typically prey on younger age classes. Deer also may be more vulnerable to predators in late winter due to stress and limited forage availability (VanCauteren and Hygnstrom 2011). Scent station records indicate that coyote populations have increased in the region in the last 2 decades (Erb 2019).

For our 2020 capture efforts, we secured permission to access 132,113 acres, consisting of 62,862 acres of private land (> 250 landowners) and 69,251 acres of public land. We expanded our partnerships with private landowners in 2020, adding an additional 15,000 acres of private land compared to the second year of the study. This study would not be possible without the enormous outpouring of support from private landowners in the study area. As in past years, we

did not attempt to capture deer in areas where USDA Wildlife Services had planned targeted culling efforts through March 2020 to decrease the likelihood that a collared deer would be culled by agency staff.

### **Sampling Design and Data Collection**

Given the breadth of the study area, we divided it into 10 quadrants (Figure 1) from which we established a baseline target goal of capturing 4-5 fawns ( $\approx$  7-9 months old) of each sex per quadrant in 2019. Our goal was to capture and collar 90 deer; 45 male fawns and 45 female fawns.

Deer were captured by net-gunning (Helicopter Wildlife Services, South Africa) from a MD500 helicopter. Once captured, all deer were collared, ear-tagged, auxiliary measurement taken (body temperature, age class, sex, and body condition), and an ear punch for genetic analysis. Helicopter pursuit time of animals did not exceed 5 minutes, and average handling time per animal was approximately 4 minutes.

We programmed GPS collars for males (Iridium TL330 with expandable collar, Lotek Wireless Inc, Newmarket, Canada) and females (Iridium 420, Lotek Wireless Inc, Newmarket, Canada) to collect location coordinates every day at an increased rate during spring dispersal and fall rut periods. For TL330 collars (males), we calibrated the rate of GPS location fixes to occur once every 117 minutes (approximately 12 per day) between 15 April through 15 July and 1 September through 15 December. During all other periods, we scheduled these collars to collect positional data every 3 hours and 45 minutes or approximately six locations per day. For Iridium 420 collars (females), we calibrated the rate of GPS location fixes to occur once every 75 minutes (approximately 19 per day) between 15 April through 15 July and 1 September through 15 December. During all other periods, we scheduled these collars to collect positional data every 2 hours and 45 minutes or approximately eight locations per day. We chose periodically higher transmission fix schedules in part based on timing of seasonal movements recorded from yearling males in Wisconsin. The expected battery life of I420 collars was longer than that of TL330 collars, and we balanced the fix rate schedules so that we had a reasonably high probability of receiving data from collared deer for at least two years (assuming deer survived and that all other collar functions remained viable). To ensure that we collected location data across the entire 24-hour day distribution, we included an offset from an hour (e.g., 1 hr 57 min or 3 hr 45 min) so programmed GPS fixes occurred on a staggered schedule that changed every day.

The collars included timed-release drop-off mechanisms, which after 130 weeks (2.5 years) will cause the collars to detach, be available for retrieval, and potentially be re-furbished. In addition, for male collars only, we included a line-of-sight mechanism that permits the collars to be detached remotely in line of sight to the animal (within 200m).

We programmed collars to transmit a mortality text message if inactive for 12 hours, and a field response was initiated within 48 hours, when possible. If a carcass was available, staff collected medial retropharyngeal lymph nodes for CWD testing, a muscle sample for potential genetic testing, and a front incisor tooth for age confirmation. In some cases, field necropsies were performed and tissue or organs samples were submitted for additional diagnostic testing at the University of Minnesota Veterinary Diagnostic Laboratory (VDL). If an animal died within the first two weeks following capture, whole carcasses were extracted and evaluated for capture myopathy. Outside of a 2-week window following capture, and after the window when capture myopathy is most likely to occur, staff performed field investigations to determine likely cause of death. Using all evidence available from a carcass (e.g., broken bones, bite marks, body condition) and the area surrounding a death site (e.g., evidence of struggle), staff assigned probabilities of cause of death including hunter-harvest, vehicle collision, capture-related issues,

underlying health conditions, indeterminate causes, agency culling, trauma, and predation/scavenging.

## **Data Analysis**

### *Survival analysis*

We estimated annual survival (Aalen-Johansen estimator; Therneau 2020) by sex using R software (R Core Team 2017) packages survival and mort, which correctly account for the staggered entry design of animals into the study over time and right censoring. If a collar failed prematurely or dropped off due to malfunctioning expansion device (males) or by accident (e.g., deer passing through a barbed wire fence), these animals were considered censored and lost to follow up from the date of occurrence. We also estimated cumulative incidence functions for cause-specific mortality (Heisey and Patterson 2006), which permits comparison of different causes of mortality in the presence of competing risks. We characterized mortality into three general causes for this analysis including hunter-harvest, vehicle collision, and other causes. The other causes category included animals that died due to underlying health conditions, indeterminate causes, agency culling, trauma, and predator/scavengers. We omitted from analysis any deer that died due to capture-related issues, defined as any mortality within 2 weeks of capture, as these animals may not be representative of the underlying deer population.

There was no protection afforded to collared deer and these animals could be legally harvested during hunting seasons or agency-culling efforts. We encouraged hunters to select animals for harvest based on their personal preference regardless of whether the hunter noticed a collar on the deer. On outreach materials, we asked hunters who harvested a collared deer to please contact MNDNR and return the collar.

### *Location data processing*

We define dispersal as having occurred if an individual displayed a permanent, asymmetric movement from a natal range to a distinct adult range (Kenward et al. 2001, 2002), such that pre-dispersal locations do not overlap post-dispersal locations (Long et al. 2005, Lutz et al. 2015). We vetted all recorded spatial locations before use in any analysis because the accuracy of a location is influenced by the number of satellites available to communicate with a collar and how a deer is juxtaposed in the landscape (i.e., influence of physical barriers); thus, any spatial location was omitted if less than three satellites were used to derive its location. These two-dimensional location coordinates resulted in highly biased altitude above sea level estimates (around 0) and high Dilution of Precision values ( $> 4$ ) indicative of inaccurate locations (generally  $> 500\text{m}$  based on controlled tests).

Locational accuracy of GPS-collars may be influenced by elevation, landform (ridgelines vs. ravines), and land cover (forests vs. open fields). For example, locational accuracy may be low when collared deer are in low elevation, forested ravines where satellite line-of-sight is inhibited. In order to better understand and correct for these potential errors, we tested collar locational accuracy in the field using 9 test collars and a Trimble GPS unit. We placed collars in 3 different land covers (forest, open fields, edges) and at relatively low (ravine) and high (ridge/hilltops) locations that were representative of the study area. For each land cover  $\times$  elevation scenario, we placed collars 6 meters apart at heights of 0.5 and 1.0 m ( $n=3$  collars each) and at ground level ( $n=3$ ). We collected collar locations every 2 hours for 2 days in each scenario. We used a Trimble Geo 7X GPS unit with a high positional accuracy within 100 cm of the true location to compare accuracy of collar locations. Across all land cover and elevation scenarios, average location error was 14 ( $\pm 15$ ) m away from the true location. Average locational error was lowest in open fields at high elevations (mean=9  $\pm$  10 m) and highest in forested ravines (mean=19  $\pm$  19 m). However, overall error did not differ significantly among cover types or

different elevations. Still, these average error rates will be taken into account in future habitat selection analyses.

Parsing location data into seasonal home ranges and dispersal events is challenging due to individual variation in movement and space use behavior among deer. Rather than parse location data into seasons based on a single calendar date for each season, we applied change point analysis to identify points of change in movement data that would signify a change in animal behavior. To identify the date(s) of spring dispersal for individual deer, we measured the Euclidean distance of each GPS location to the animal's original capture location. We used the *meanvar* function in the *changept* package in R to identify points of change in the distance of each location to the original capture location. We limited the change point analysis to five points and set the minimum bin number to 10 locations within which to calculate mean and variance. We used five change points because we found that five points effectively captured abrupt changes in distance to capture location that represented dispersal movements in the spring, as well as seasonal migrations and home range expansions during fall and winter. The first change point typically represented a spring dispersal event. We used dates of change points to identify dispersal events and parse out periods of movement from those of stationary space use.

#### *Home range analysis*

After removing locations during dispersal or travel periods, we estimated the size of the 95% kernel density isopleth, the area in which the deer spent 95% of its time (hereafter, *home range*). For ease of interpretation, we assigned each location to a season using average dates of first and last snowfall, along with average growing season dates; growing season (GS): 01 May – 31 Aug., fall (FA): 01 Sept.- 15 Nov., and winter (WN): 16 Nov.- 30 Apr. We calculated seasonal home ranges to evaluate the hypothesis that home ranges would expand in the fall, as both sexes increased movements in search of potential mates. However, for simplicity, we also calculated the annual home range size for each deer by averaging seasonal home range sizes. We hypothesized that home ranges would expand in the fall in order to seek mates. To examine potential environmental influences on home range size, we calculated the proportion of row-crop agriculture in each home range using the 2016 National Land Cover Database (USDA 2018) and the spatial join tool in ArcGIS. We also calculated the proportion of agriculture in the township in which each home range was centered. We chose the proportion of agriculture over other cover types because it was the most consistently available across the study area; forest cover was rare in many townships in the western portion of the study area. In addition, forest and agriculture were highly negatively correlated ( $r=-0.97$ ,  $p<0.001$ ) within home ranges.

We evaluated differences in the size of home ranges by sex, season, year and land cover covariates using linear mixed effects models. We specified season, sex, and year as fixed effects and the individual deer as a random effect to account for >1 seasonal home ranges per deer. We used AICc model selection to assess support for explanatory models in separate model sets. For each kernel isopleth, we evaluated a global additive model that included season, sex, year and land cover covariates, a global model that included an interaction between season and sex, and separate models of each variable alone. We compared these models to a null model that only included the random effect of the individual deer. We considered the top-ranked model and any models within two AICc units of the top model to be competitive (Burnham and Anderson 2002).

#### *Movement analysis*

We identified dispersal and other movements outside of the home range using change point analysis and then assigned those movements to one of three categories: natal dispersal,

seasonal migration, or temporary excursions. For each movement, regardless of type, we measured the straight-line distance of the movement, the overall direction of the movement (1 of 4 cardinal directions), and the dates and duration of the movement. For natal dispersal, we calculated the straight-line distance between the adult home range and natal home range centroids (Kenward et al. 2002). We performed all spatial data analysis and characterization using packages *adehabitatHR* (Calenge 2006), *sp*, and *rgdal* within R software (R Core Team 2017), and ArcMap 10.6 (Environmental Systems Research Institute, Redlands, CA, USA).

## RESULTS AND DISCUSSION

From 8-12 February 2020, we captured and outfitted 56 deer with Iridium GPS collars: 31 female fawns and 25 male fawns (Figure 1). Following initial capture and collar fitting, two male and two female fawns were able to immediately kick off their collars, resulting in a final 2020 release cohort of 52 fawns ( $n=29$  females, 23 males). Our original goal was to capture 90 fawns (equal sex ratio), and the shortfall occurred because the helicopter capture company experienced significant difficulties in the field and did not capture deer at a rate that would ensure completion of the quota within a timely manner, leaving 42 GPS collars that were not deployed.

As of June 16, 2020, we are monitoring 27 female and 19 male deer from the 2020 release cohort. There have been two collar failures of unknown cause from this cohort. A total of 90 collars from the 2018 release cohort and 17 collars from the 2019 cohort have been deactivated due to either failure or battery senescence. Two additional animals from the 2020 cohort dropped their collars by accident (likely due to moving through barbed wire fences). In total, we are actively monitoring 74 GPS-collared deer from all years of the study, including 46 females (19 from 2019, and 27 from 2020) and 28 males (9 from 2019 and 19 from 2020).

### Data Analysis

#### *Survival analysis*

To date there have been 82 known mortalities due to hunter-harvest ( $n=36$ ), vehicle collision ( $n=12$ ), capture-related issues ( $n=12$ ), underlying health conditions ( $n=6$ ), indeterminate causes ( $n=6$ ), agency culling ( $n=4$ ), trauma ( $n=4$ ), and predation/scavenging ( $n=2$ ) (Figure 2). It is important to note that five of 12 deer ascribed to an indeterminate cause of death wore GPS collars that failed after deployment, so we never received a mortality signal to follow up with carcass investigations. Instead, in these cases, either landowners or hunters happened by chance upon skeletal remains in the field preventing us from ascribing a source of mortality. We estimated average survival by year and sex (Figure 3) and grouped causes of mortality as hunter-harvest, vehicle collision, and other (all other causes) in order to estimate annual cumulative incidence curves. Average annual survival for females and males was 0.73 (CI: 0.62-0.86) and 0.54 (CI: 0.40-0.73), respectively, and the difference was marginally significant ( $Z=1.80$ ;  $P=0.07$ ). Average annual mortality due to hunter harvest was 18%, while that for other causes and vehicle collision were 11% and 6%, respectively (Figure 4). After adjusting for multiple comparisons using a Bonferroni correction, hunter harvest was significantly greater than vehicle collision ( $Z=2.37$ ;  $P=0.05$ ), but not other causes ( $Z=1.19$ ;  $P=0.71$ ). Other causes of mortality were not significantly different from vehicle collision ( $Z=1.28$ ;  $P=0.60$ ).

We captured deer when they were older fawns, at least 7-9 months old, therefore, our survival estimates are conditional on animals surviving through this age. Furthermore, our study only reflects two years of survival data, and the upper limit on age classes reflected is around 3.5 years. Deer typically experience the highest risk of mortality after birth through the first year of life (DelGiudice et. al. 2006), so our estimates do not capture the period when deer are most vulnerable. Several neonate studies in the upper Midwest have shown that fawn mortality during

the first few months of life for white-tailed deer was driven by predators or natural causes (Brinkman et al. 2004, Carstensen et al. 2009, Grovenburg et al. 2011, Warbington et al. 2017). Research in Minnesota has shown that winter severity index and wolf predation can be significant sources of mortality for deer, particularly in the northern forest region (DelGiudice et al. 2006). However, in our study area, sources of mortality are more aligned with patterns observed in southwestern Minnesota and other parts of the Midwest, where hunter harvest and deer-vehicle collisions are the primary causes in adult deer (Brinkman et al. 2004, VerCauteren and Hygnstrom 2011, Krebs 2014). Our survival estimates appear to be low and, taken at face value, would yield an average life expectancy of about 4.5 years and 2.5 years for females and males, respectively. However, these estimates potentially reflect several processes at work. Our sample purposely focuses on a narrow range of age classes, primarily yearling deer, because we sought to investigate dispersal patterns. It is well known that yearling and 2.5 year-old males are the most vulnerable age-sex class to hunter harvest (Roseberry and Klimstra 1974, McCullough 1979, Nixon et al. 1994). To facilitate CWD management efforts, in 2017 antler point restrictions (APR) were removed from Deer Permit Area (DPA) 603 and unlimited antlerless tags were available for a nominal fee, which represented a small subset of our study area. In 2019, MNDNR dissolved DPA 603 into a broader CWD Management Zone, and removed APR and liberalized harvest throughout our entire study area. The possible effect of this liberalized harvest regulation change may be reflected in lower male survival during 2019 compared with 2018 (Figure 3). Potentially adding to this effect, it is possible that hunters selectively harvested collared deer at a higher rate (Jacques et al. 2011), thus biasing our annual survival estimates low.

### *Home range analysis*

We have amassed over 450,000 records of deer location data from 23 March 2018 through 17 June 2020. Of 148 deer monitored in 2018 and 2019, 127 survived long enough to collect sufficient GPS location data to estimate areas of activity for at least one season (62 females and 65 males). Average home range size was 1.75 km<sup>2</sup> (CI: 1.37-2.13) and 2.21 km<sup>2</sup> (CI: 1.72-2.70) for females and males, respectively. These estimates fall in line with our expectations and home range sizes for other deer in the Midwest (Walter et al. 2009).

We evaluated 8 models that included season, sex, year, and the proportion of row-crop agriculture to explain variation in home range size. The full model received 87% of model support, followed by the full model with an interaction between season and sex (Table 1). The top-ranked model indicated that deer home ranges were significantly smaller during the growing season [ $\beta_{GS} = -1.75 \pm 0.34$ ; CI: -2.43-(-1.08)]; Figure 4) and winter [ $\beta_{WN} = -1.16 \pm 0.37$ ; CI: -1.89-(-0.43)] compared to fall (Figure 5). In addition to seasonal differences, home range size increased with increasing proportions of row-crop agriculture within home ranges ( $\beta_{crop} = 2.46 \pm 0.68$ ; 95% CI: 1.13-3.78; Figure 5). Males had somewhat larger home ranges, but this difference was not significant ( $\beta_{male} = 0.48 \pm 0.25$ ; CI: -0.02-0.98). The proportion of row-crop agriculture within the township did not appear to influence home range size ( $\beta_{crop\_township} = 0.57 \pm 0.65$ ; CI: -0.70-1.85).

Our estimates of home range size are well within estimates for white-tailed deer in other regions of the Midwest and eastern U.S. (Walter et al. 2009, Magle et al. 2015, Walter et al. 2018). Home range size is influenced by several environmental factors, including forest connectivity and landscape composition (Magle et al. 2015, Walter et al. 2018). In forested landscapes, home ranges tend to increase with increasing homogeneity of land cover and lower forest edge density (Walters et al. 2018). In southcentral Wisconsin, a mixed agricultural-forested region similar to our study area, Magle et al. (2015) also found that home ranges increased with

increasing proportion of agricultural land cover with the home range. In southeastern Minnesota, the predominance of row-crop agriculture, especially in the western portion of the study area, naturally results in larger home ranges, as deer must travel farther to meet food and cover needs found in forests and open habitats.

Home range dynamics can influence transmission and spread of CWD at the local scale within a population. Local spread may be influenced by social group dynamics, home range overlap, and relatedness, all of which can affect the rate of direct and indirect transmission of CWD prions among deer (Magle et al. 2013, Schaubert et al. 2015, Tosa et al. 2017, Koen et al. 2017). Risk may change seasonally as well, as deer expand or contract their home ranges during the fall rut and fawning seasons, respectively (Koen et al. 2017). At the larger population level, there is some evidence that landscape connectivity can increase the social network of deer, thus providing a conduit for longer distance spread of CWD (Norbert et al. 20, Koen et al. 2017). In particular, Koen et al. (2017) found that the social connectivity among deer increased with agricultural lands and connectivity of edge. In our study, the relationship between greater proportions of agricultural land and larger home ranges may result in a larger and more connected social network, but more research on home range overlap may be needed to fully understand the relationship between home range size and social network connectivity among deer in Minnesota.

#### *Movement analysis*

For all deer available in the study with sufficient data we found that 26% (n=16/61) of females and 43% (n=23/54) of males dispersed between their natal and adult home range, yet this difference was marginally significant ( $\chi^2=2.73$ ,  $P=0.10$ ). We also determined that 15% (n=9/61) of females and 6% (n=3/54) of males underwent apparent seasonal migration between summer and winter ranges, although there was no significant difference between these proportions ( $\chi^2=1.70$ ,  $P=0.19$ ). The average dispersal distance traveled for females and male was 20.0 km (CI: 5.67-30.10) and 22.8 km (CI: 11.70-32.30), respectively. The average one-way distance traveled for migratory females and males was 12.8 km (CI: 3.49-18.40) and 17.7 km (CI: 1.35-27.20), respectively. The pattern in dispersal distance traveled was consistent between years, and suggests that females are just as likely to disperse from their natal range and travel approximately the same average distance as males. The number of animals performing apparent migratory movements was too small to detect general patterns, and it is not clear if these movements were driven by some evolutionary or proximate resource cause. We observed more extreme dispersal distances by both sexes, with the maximum linear distance traveled by a female and male of 116 km and 97 km, respectively. While these extreme distances are outliers, deer have been reported to travel similar long distances in other agricultural landscapes (Kernahan et al. 1994, Nixon et al. 2007). In other work done in agricultural landscapes of Illinois, average dispersal distances were approximately 30 km and males and females dispersed at approximately equal rates (Nixon et al. 2007). Many animals in the study conducted temporary excursions from their home range, lasting hours to several days. It is not clear yet whether the timing of these excursions are clustered during particular seasons, but it is likely that these type of movements are important in the process of intragroup disease transmission at a local spatial scale. We are currently in the process of analyzing these movements to find any patterns that might emerge.

The variation in dispersal behavior that we observed in southeastern Minnesota reflects the transition in landscape features across the study area. Our study occurred in a region of southeastern Minnesota that transitions from the eastern forested bluff and ridge country along

the Mississippi into the row-crop agriculture in the western part of the study area. As found in southwestern Minnesota where a significant proportion of deer perform seasonal migrations initiated by severe weather (Brinkman et al 2005), we observed seasonal migrations for some animals in the southwestern part of our study area. These deer spent the summer months in northern Iowa and returned to Minnesota in winter. A study conducted in the 1980s around Whitewater Wildlife Management Area in southeastern Minnesota using radio telemetry showed that some deer migrated between Minnesota and Wisconsin (Simon 1986). We have not observed such interstate movements in our study to date and most deer have not exhibited seasonal migration patterns.

While male dispersal typically is regarded as the primary force driving potential disease spread (CWD) on the landscape (Gear et al 2006, Oyer et al. 2007), evidence suggests that high underlying deer density (Lutz et al. 2015) can drive females to disperse. Approximately half of all collared deer dispersed in the study. Given the relatively high rate and extent of female dispersal and high pre-fawn deer densities in the farmland-forest transition zone of our study area at around 42 deer/mi<sup>2</sup> (E. Michel, pers. comm.), we hypothesize that density-induced dispersal may be occurring in southeastern Minnesota. This highly productive landscape favors high deer survival and fecundity, given extensive food resources, winter cover, and relatively mild winters. Additional study of deer representative of southeastern Minnesota will further inform our understanding of dispersal and movement activities as it relates to potential spread of CWD prions on the Minnesota landscape.

Effective communication about this study to project participants is essential for our success. We have provided outreach materials both for landowners that have provided us with permission to use their properties for deer capture and for the general public. We continue to inform participating landowners twice per year with deer movement updates and maps of the collared deer in the study, and provide a summary of study findings and expectations for future work. Similarly, we continue to update a dedicated website to this research project at <https://www.dnr.state.mn.us/cwd/deer-movement-study.html>. This site provides information about the purposes of the study, periodic updated findings, and information about how readers can assist and contribute to our efforts. We encourage the public to provide us with trail camera photos of collared deer they may encounter, and with their permission, we make these pictures available on our website. There have also been almost two dozen popular press articles covering this study in various media outlets. Overall, we strive to continually improve how we communicate science to the public, and provide transparency in all of the work that we conduct.

### **Future Capture and GPS-Collaring Efforts**

We have approximately 45 Lotek GPS collars available to deploy in winter 2021, and plan to contract again with a wildlife helicopter capture company to conduct capture and collaring efforts. We will aim to collect equal sample sizes between sexes and focus more effort in Houston County on the border with Wisconsin. This would fill a major gap in the spatial coverage of our samples thus far, and perhaps reveal important movements of deer between Minnesota and Wisconsin.

### **ACKNOWLEDGMENTS**

We extend warm thanks to all of the participating landowners in southeastern Minnesota that gave us permission to access and conduct capture operations on their properties. We are grateful to our DNR colleagues Margaret Dexter, Todd Froberg, Patrick Hagen, Erik Hildebrand, Kelsie LaSharr, Tyler Obermoller, and Ryan Tebo for their participation in field activities and technical support. We thank all the MNDNR Wildlife and Enforcement staff, who assisted in contacting landowners and fielding questions about the study to the public including Don

Ramsden, Mike Tenney, and Mitch Boyum. Special thanks to Julie Hines and Bob Wright for their great work assisting us with our GIS mapping needs; Nyssa Gesch and Chris Scharenbroich for their efforts with helping us update the webpage dedicated to this project on the DNR website; Rushford Municipal Airport and Fillmore County Airport in Preston, Minnesota for use of their facilities. Without the support of these and many more people behind the scenes, this project would not be possible. We also thank LCCMR – the Environment and Natural Resource Trust Fund (ENRTF) - Emerging Issues account (M.L. 2015, Chp. 76, Sec. 2, Subd. 10) that we received grant funding from provided the needed funds to get this project off the ground. Additional funding was provided in part by the Wildlife Restoration (Pittman-Robertson) Program.

## LITERATURE CITED

- Almberg, E. S., P. C. Cross, C. J. Johnson, D. M. Heisey, B. J. Richards. 2011. Modeling routes of chronic wasting disease transmission: Environmental prion persistence promotes deer population decline and extinction. *PLoS One* <https://doi.org/10.1371/journal.pone.0019896>
- Breed, D., L. C. R. Meyer, J. C. A. Steyl, A. Goddard, R. Burroughs, and T. A. Kohn. 2019. Conserving wildlife in a changing world: Understanding capture myopathy—a malignant outcome of stress during capture and translocation. *Conservation Physiology* 7: doi:10.1093/conphys/coz027.
- Brinkman, T. J., C. S. DePerno, J. A. Jenks, B. S. Haroldson, and R. G. Osborn. 2005. Movement of female white-tailed deer: Effects of climate and intensive row-crop agriculture. *Journal of Wildlife Management* 69:1099-1111.
- Brinkman, T. J., J. A. Jenks, C. S. DePerno, B. S. Haroldson, and R. G. Osborn. 2004. Survival of white-tailed deer in an intensively farmed region of Minnesota. *Wildlife Society Bulletin* 32:726–731.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag, New York, 488 pages.
- Calenge, C. 2006. The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197:516-519.
- Carstensen, M., G. D. DelGiudice, B. A. Sampson, and D. W. Kuehn. Survival, birth characteristics, and cause-specific mortality of white-tailed deer neonates. *Journal of Wildlife Management* 73:175-183.
- DelGiudice, G. D., J. Fieberg, M. R. Riggs, M. Carstensen Powell, and W. Pan. 2006. A long-term age-specific survival analysis of female white-tailed deer. *Journal of Wildlife Management* 70:1556-1568.
- DeVivo, M. T., D. R. Edmunds, M. J. Kaufmann, B. A. Schumaker, J. Binfet, T. Kreeger, B. Richards, H. M. Schatzl, and T. E. Cornish. 2017. Endemic chronic wasting disease causes mule deer population decline in Wyoming. *PLoS One* 12(10): e0186512.
- Edmunds, D.R., M.J. Kauffman, B.A. Schumaker, F.G. Lindzey, W.E. Cook, T.J. Kreeger, R.G. Grogan, and T.E. Cornish. 2016. Chronic wasting disease drives population decline of white-tailed deer. *PLoS One* <https://doi.org/10.1371/journal.pone.0161127>
- Erb, J. 2019. Carnivore scent station survey summary, 2019. Minnesota Department of Natural

Resources. Available at <https://www.dnr.state.mn.us/recreation/hunting/trapping/index.html>.

- Grear, D. A., M. D. Samuel, J. A. Langenberg, and D. Keane. 2006. Demographic patterns and harvest vulnerability of chronic wasting disease infected white-tailed deer in Wisconsin. *Journal of Wildlife Management* 70:546-553.
- Grovenburg, T. W., C. N. Jacques, C. S. DePerno, R. W. Klaver, and J. A. Jenks. 2011. Female white-tailed deer survival across ecoregions in Minnesota and South Dakota. *American Midland Naturalist* 165:426-435.
- Heisey, D. M., and B. R. Patterson. 2006. A review of methods to estimate cause-specific mortality in presence of competing risks. *Journal of Wildlife Management* 70:1544-1555.
- Jacques, C. N., T. R. Van Deelen, W. H. Hall Jr., K. J. Martin, and K. C. VerCauteren. 2011. Evaluating how hunters assess and react to telemetry collars on white-tailed deer. *Journal of Wildlife Management* 75: 221-231.
- Kenward, R. E., S. P. Rushton, C. M. Perrins, D. W. MacDonald, and A. B. South. 2002. From marking to modeling: Dispersal study techniques for land vertebrates. Pp. in *Dispersal Ecology* (Bullock, J. M., Kenward, R. E., Hails, R. S., eds). Blackwell Publishing, Maiden Massachusetts.
- Kenward, R.E., S.S. Walls, and K.H. Hodder. 2001. Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances? *Journal of Animal Ecology* 70:1-13.
- Kernohan, B. J., J. A. Jenks, and D. E. Naugle. 1994. Movement patterns of white-tailed deer at Sand Lake National Wildlife Refuge, South Dakota. *Prairie Naturalist* 26:293-300.
- Koen E. L. M. I. Tosa, C. K. Nielsen, and E. M. Schaubert. 2017. Does landscape connectivity shape local and global social network structure in white-tailed deer? *PLoS ONE* 12(3): e0173570. <https://doi.org/10.1371/journal.pone.0173570>
- Krebs, N. New Wisconsin study reveals data on deer mortality. *Outdoor Life*. Accessed on 6/17/20. <https://www.outdoorlife.com/blogs/newshound/2014/01/new-wisconsin-study-reveals-data-deer-mortality/>.
- Long, E. S., D. R. Diefenbach, B. D. Wallingford, and C. S. Rosenberry. 2010. Influence of roads, rivers, and mountains on natal dispersal of white-tailed deer. *Journal of Wildlife Management* 74:1242-1249.
- Long, E. S., D. R. Diefenbach, C. S. Rosenberry, and B. D. Wallingford. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. *Behavioral Ecology*: 1235-1242.
- Long, E. S., D. R. Diefenbach, C. S. Rosenberry, B. D. Wallingford, and M. D. Grund. 2005. Forest cover influences dispersal distance of white-tailed deer *Journal of Mammalogy* 86:623-629.
- Lutz, C. L., D. R. Diefenbach, and C. S. Rosenberry. 2015. Population density influences dispersal in female white-tailed deer. *Journal of Mammalogy* 96:494-501.
- Magle, S. B., M. D. Samuel, T. R. Van Deelen, S. J. Robinson, and N. E. Mathews. Evaluating spatial overlap and relatedness of white-tailed deer in a chronic wasting disease management zone. *PLoS ONE* 8: e56568. <https://doi.org/10.1371/journal.pone.0056568>.
- Magle, S. B., L. H. Kardash, A. Oyer Rothrock, J. C. Chamberlin, and N. E. Mathews. 2015. Movements and habitat interactions of white-tailed deer: implications for chronic wasting

- disease management. *The American Midland Naturalist* 173: 267–82.  
<https://doi.org/10.1674/amid-173-02-267-282.1>.
- McCullough, D. R. 1979. *The George Reserve Deer Herd: Population Ecology of a K Selected Species*. Ann Arbor, MI: University of Michigan.
- Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist* 37:223-249.
- Nixon, C. M., L. P. Hansen, P. A. Brewer, J. E. Chelsvig, J. B. Sullivan, T. L. Esker, R. Korkenmeier, D. R. Etter, J. Cline, J. A. Thomas. 1994. Behavior, dispersal and survival of male white-tailed deer in Illinois. *Illinois Natural History Survey Biological Notes* 139.
- Nixon, C. M., P. C. Mankin, D. R. Etter, L. P. Hansen, P. A. Brewer, J. E. Chelsvig, T. L. Esker, and J. B. Sullivan. 2007. White-tailed deer dispersal behavior in an agricultural environment. *American Midland Naturalist* 157: 212-220.
- Oyer, A. M., N. E. Mathews, and L. H. Skuldt. 2007. Long distance movement of a white-tailed deer away from a chronic wasting disease area. *Journal of Wildlife Management* 71:1635-1638.
- Peterson, B. E., D. J. Storm, A. S. Norton, and T. R. Van Deelen. 2017. Landscape influence on dispersal of yearling male white-tailed deer. *Journal of Wildlife Management* 81: 1449-1456.
- R Core Team. 2017. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Roseberry, J. L., and W. D. Klimstra. 1974. Differential vulnerability during a controlled deer harvest. *Journal of Wildlife Management* 38: 499-507.
- Samuel, M. D., and D. J. Storm 2016. Chronic wasting disease in white-tailed deer: infection, mortality, and implications for heterogeneous transmission. *Ecology* 97: 3195-3205.
- Schauber, E. M., C. K. Nielsen, L. J. Kjær, C. W. Anderson, and D. J. Storm. 2015 Social affiliation and contact patterns among white-tailed deer in disparate landscapes: implications for disease transmission. *Journal of Mammalogy* 96: 16-28. doi:10.1093/jmammal/gyu027
- Simon, D. E. 1986. Density, migration, and mortality patterns of white-tailed deer using a sanctuary in southeastern Minnesota. M. S. thesis. University of Minnesota. 66 pages.
- Tosa, M. I., E. M. Schaubert, and C. K. Nielsen. 2017. Localized removal affects white-tailed deer space use and contacts. *Journal of Wildlife Management* 81: 26-37.  
<https://doi.org/10.1002/jwmg.21176>
- Therneau, T. 2020. A Package for Survival Analysis in R. R package version 3.2-3,  
<https://CRAN.R-project.org/package=survival>.
- VerCauteren, K., and S. E. Hygnstrom. 2011. Managing white-tailed deer: Midwest North America. *In* *Biology and Management of White-tailed Deer* (ed. D. G. Hewitt). CRC Press, Boca Raton.
- Walter, W. D., S. E. Tyler, D. Stainbrook, B. D. Wallingford, C. S. Rosenberry, and D. R. Diefenbach. 2018. Heterogeneity of a landscape influences size of home range in a North American cervid. *Scientific Reports* 8: 14667. <https://doi.org/10.1038/s41598-018-32937-7>.

Walter, W. D., K. C. VerCauteren, H. Campa, III, W. R. Clark, J. W. Fischer, S. E. Hygnstrom, N. E. Mathews, C. K. Nielsen, E. M. Schauber, T. R. Van Deelen, and S. R. Winterstein. 2009. Regional assessment on influence of landscape configuration and connectivity on range size of white-tailed deer. *Landscape Ecology* 24: 1405–1420.

Warbington, C. H., T. R. Van Deelen, A. S. Norton, J. L. Stenglein, D. J. Storm, and K. J. Martin. 2017. Cause-specific neonatal mortality of white-tailed deer in Wisconsin, USA. *Journal of Wildlife Management* 81:824-833.

Wisconsin DNR. 2018. The newsletter of the southwest Wisconsin CWD, deer and predator study. Issue 4, February 2018.  
<https://dnr.wi.gov/topic/research/articles/february2018.html#articleOne>.

Table 1. Factors associated with size of 95% home ranges among deer (n=127) monitored with GPS collars 2018-2020 in southeast Minnesota. Home range sizes were fitted to linear mixed effects models with explanatory variables as fixed effects and the deer id as a random effect.

Model	df	AICc	$\Delta$ AICc	$w_i$
HR~ Season + Sex + Year + p(crop) <sup>a</sup> + p(crop_township) <sup>b</sup>	9	2449.79	0.00	0.87
HR~ Season*Sex + Year + p(crop) + p(crop_township)	11	2453.64	3.85	0.13
HR~ p(crop_township)	4	2484.73	34.94	0.00
HR~ p(crop)	4	2550.19	100.40	0.00
HR~ Season	5	2551.18	101.39	0.00
HR~ Season*Sex	8	2552.95	103.16	0.00
HR~ Sex	4	2566.83	117.04	0.00
HR~ (.)*	3	2570.06	120.27	0.00

<sup>a</sup>Proportion of row-crop agriculture within the home range.

<sup>b</sup>Proportion of row-crop agriculture within the township.

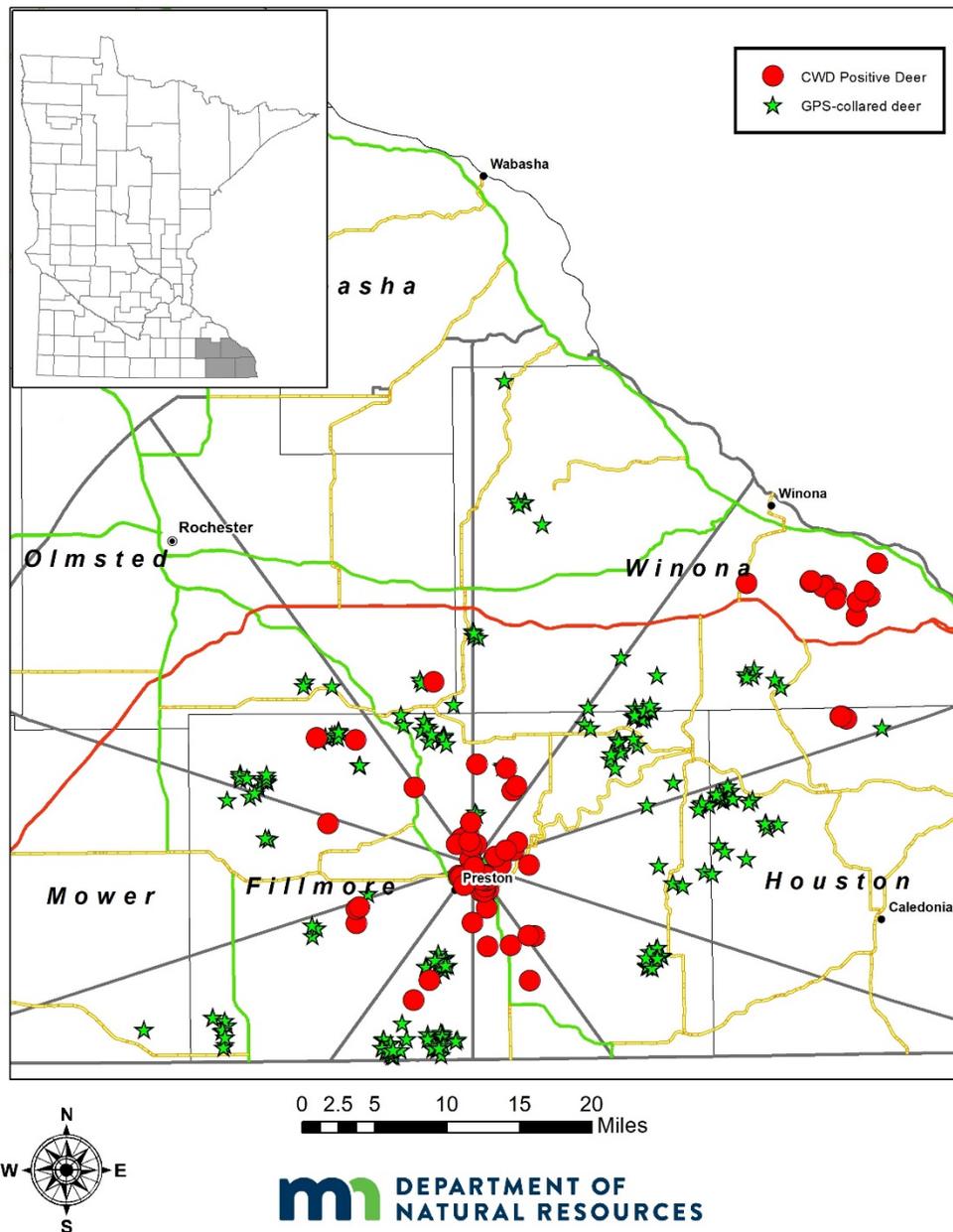
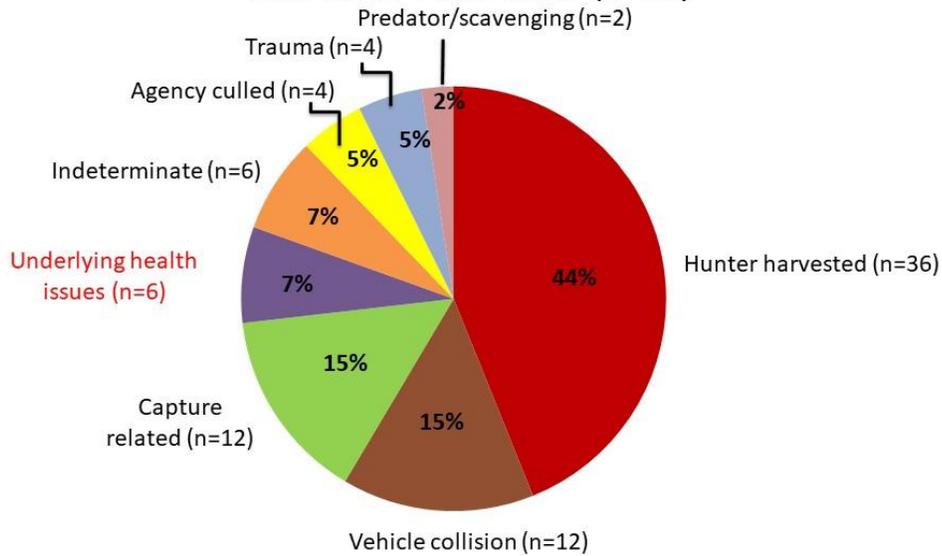


Figure 1. Spatial distribution of all deer captured and GPS-collared in southeastern Minnesota during March 2018 (n=109), February 2019 (n=64), and February 2020 (n=52). We captured deer on private and public lands, with a goal of capturing equal sex ratios across each quadrant. Green stars represent the locations where white-tailed deer were captured, fitted with GPS collars, and released. Also presented is the spatial distribution of wild white-tailed deer confirmed with CWD infection in southeastern Minnesota as of 07/26/20. There have been 85 wild white-tailed deer confirmed positive with CWD in southeastern Minnesota since fall 2016.

A)

### Proximate Causes of White-tailed Deer Mortalities

Mar 2018-June 2020 ( $n=82$ )



B)

### Causes of Deer Mortalities – Underlying health conditions

Mar 2018-June 2020 ( $n=6$ )

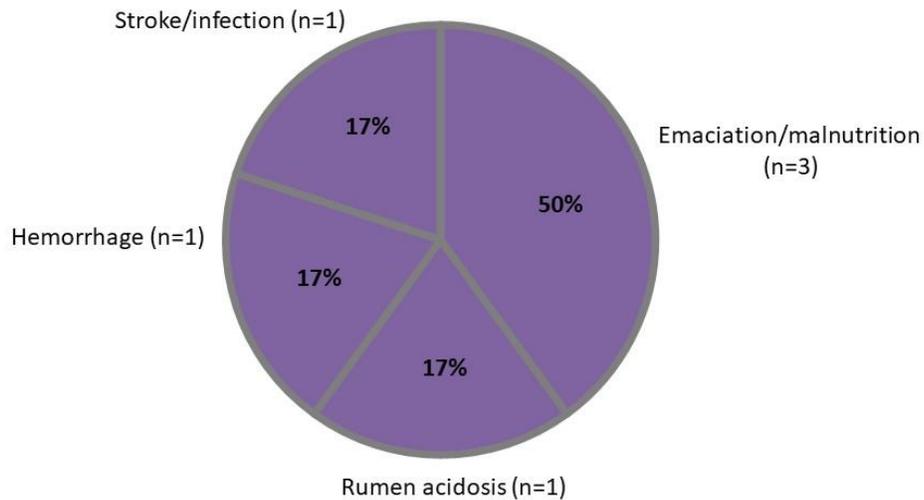


Figure 2. A) Causes of known mortality for 82 collared yearling and adult deer from March 2018 through June 2020 in southeastern Minnesota. Hunter harvest represents the primary source of mortality. B) Within the category of underlying health condition, we identified more detailed causes of mortality.

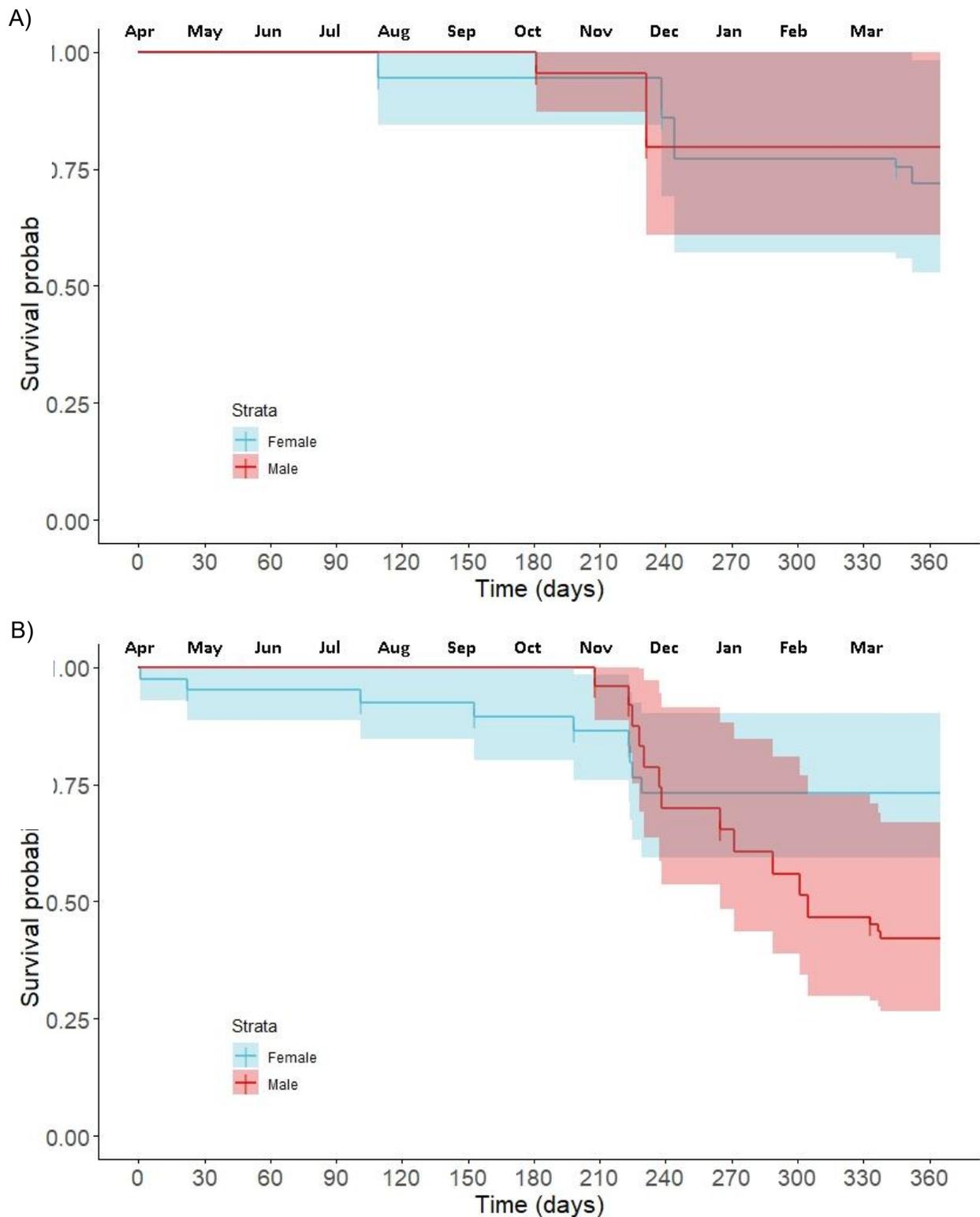


Figure 3. A) Estimated survival (and 95% CI) by sex for collared white-tailed deer in southeastern MN from 1 April 2018 through 31 March 2019. B) Estimated survival (and 95% CI) by sex for collared white-tailed deer in southeastern MN from 1 April 2019 through 31 March 2020.

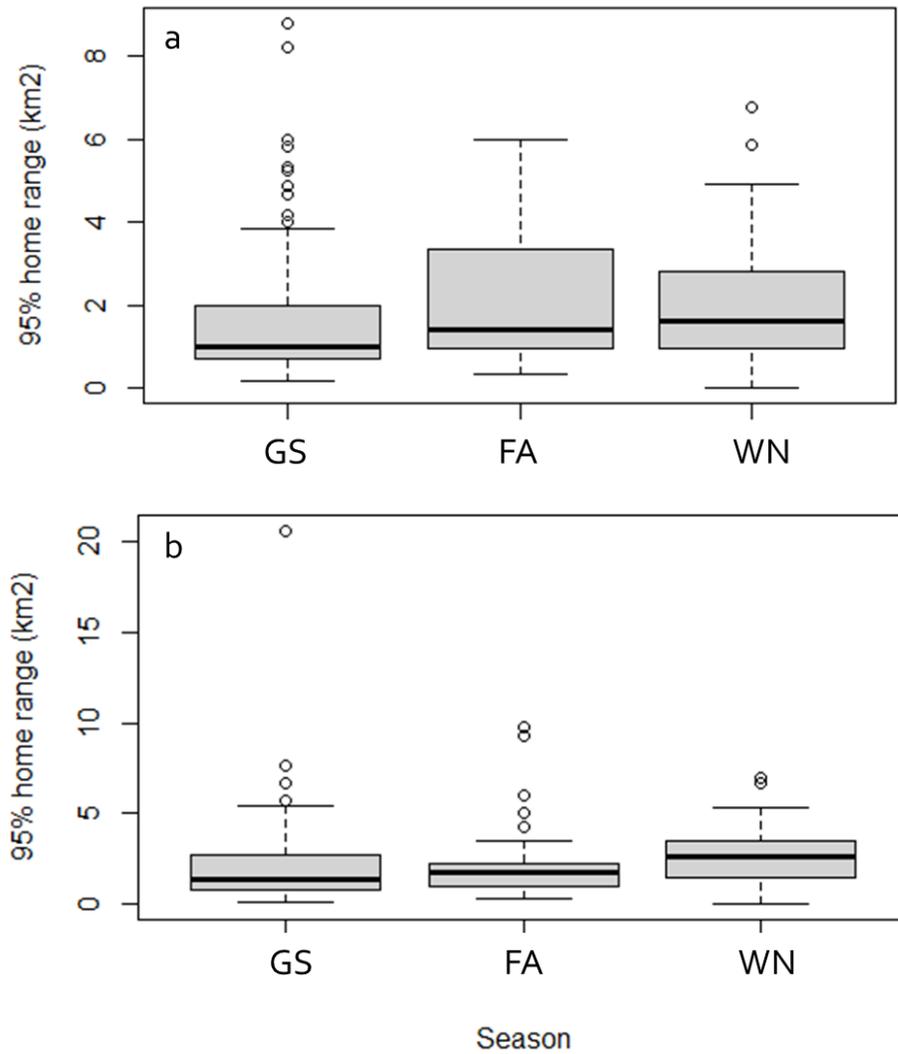


Figure 4. Distribution of 95% home range sizes (km<sup>2</sup>) by season for female (a) and male (b) white-tailed deer collared and monitored in southeastern Minnesota, 2018-2020. GS=Growing Season; 01 May–31 Aug. of each year; FA=fall; 01 Sept. – 15 Nov., WN=Winter; 16 Nov.–30 Apr of each year. Season dates were set using first and last snowfall dates and frost-free dates.

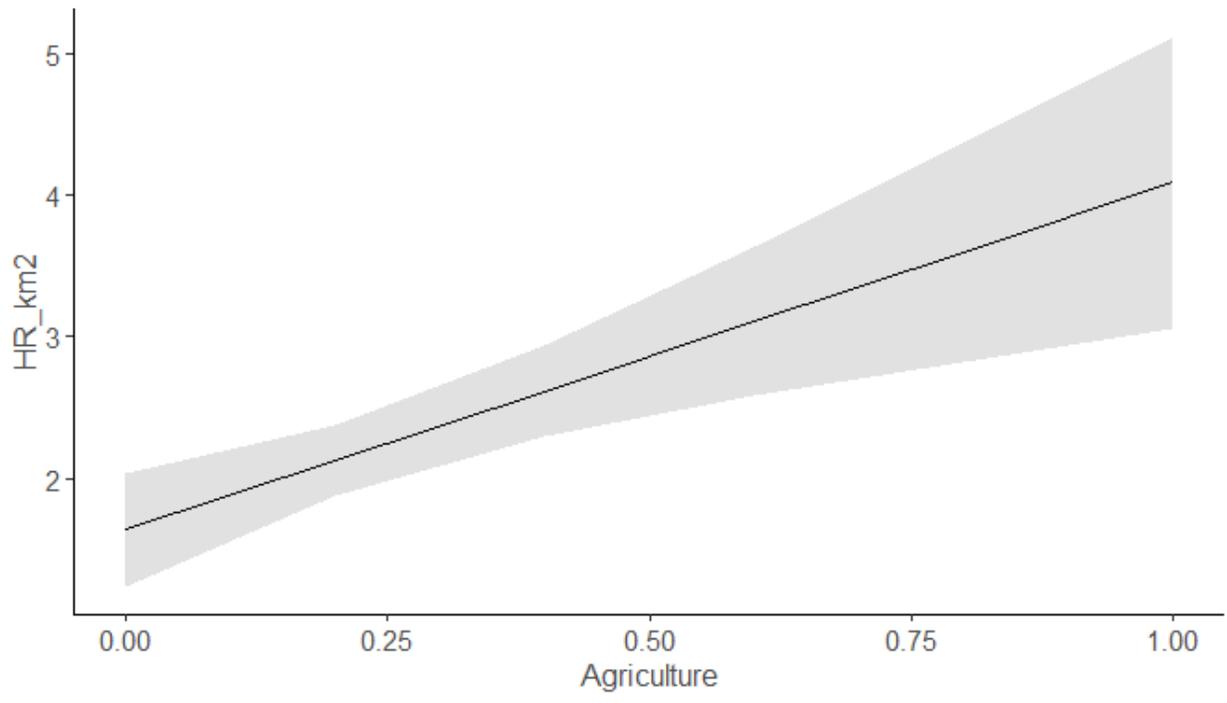


Figure 5. Model-derived estimates of home range sizes with increasing proportion of row-crop agriculture within home ranges on home range size for white-tailed deer (n=127) collared and monitored in southeastern Minnesota, 2018-2020.