

Remote Camera-traps as a Management Tool: Estimating Abundance and Landscape
Effects on the Density of White-tailed Deer

A Thesis Submitted to the Committee of Graduate Studies in Partial Fulfillment of the
Requirements for the Degree of Master of Science in the Faculty of Arts and Science

TRENT UNIVERSITY
Peterborough, Ontario, Canada
©Copyright by Grace Anne Bullington 2023
Environmental and Life Science M.Sc. Graduate Program
January 2024

Abstract

Remote Camera-traps as a Management Tool: Estimating Abundance and Landscape Effects on the Density of White-tailed Deer

Grace Anne Bullington

Quantifying the impacts of environmental conditions on the abundance of wildlife populations is important for making informed management decisions in the face of increasing environmental threats. Managers require robust tools to estimate abundance and density of wildlife rapidly and with precision. Within the context of studying white-tailed deer, I evaluated the use of camera-traps and a recently developed spatial-mark resight model to estimate deer density and evaluate habitat and land use factors influencing deer density. The study was conducted in central Ontario, Canada on approximately 16 km² of public land including the protected Peterborough Crown Game Preserve. Telemetry locations from 39 radio-collared deer were used and one hundred camera-traps were deployed for a total of 140 days from January 2022 to May 2022. Using telemetry locations and camera-trap photos I built a two-step spatial-mark resight model to estimate deer density. Deer density varied during the study as a portion of the population migrated to wintering areas outside of the study area. Despite fluctuations in precision, estimates improved towards the end of the study as more data became available and deer space use stabilized. The average deer density during the entire study was 3.0 deer/km² (95% CI= 0.1, 5.8; SD= 1.7; CV= 55%; N= 238 deer). The lowest mean density was 0.2 deer/km² (95% CI= 0.1, 0.4; SD= 0.1; CV= 50%; N= 15 deer) from February 26th to March 11th and the highest mean density was 4.8 deer/km² (95% CI= 3.1, 6.2; SD= 0.8; CV= 17%; N= 378 deer) from May 7th to May 20th. When I incorporated

spatial covariates into the model to estimate effects on deer density, higher proportions of mixed forest, deciduous forest, and road and trail density all had negative effects on deer density. While models contained some uncertainty, deer density appeared higher in the portion of the study area protected from licensed hunting. This thesis provides a framework for managers to use camera-traps and the spatial-mark resight model to monitor deer populations and link environmental covariates to spatial variation in density. As environmental threats such as habitat loss and infectious diseases increase in severity, monitoring wildlife population numbers will be vital for informed responses to these threats. The two-step spatial-mark resight model with environmental covariates provides managers with a long-term monitoring tool to evaluate management efforts and population health in forested areas.

Keywords: white-tailed deer, spatial-capture recapture, camera-trap, density estimation, wildlife management, chronic wasting disease, landscape ecology, population estimation

Acknowledgements

First and foremost, I would like to thank my graduate advisors, Joe Northrup and Brent Patterson. They have helped me to grow as a research biologist by providing their expertise, guidance, and advice. Thank you for helping me see this project to completion, from the early stages of camera deployment to the final review of this thesis. Despite setbacks, changes in research objectives, and general uncertainty (thanks to a global pandemic) your patience and support never wavered. Your approach to applied wildlife research is inspiring and it has been a privilege to work with and learn from you. Additional thanks to the third member of my thesis committee, Jim Schaefer, who has always provided insightful and refreshing perspectives on this thesis.

I would not have been able to complete this thesis without the help of the Ontario Ministry of Natural Resources and Forestry research staff. Deploying, maintaining, and reviewing the images from 100 camera-traps would not have been possible without the help of the technicians and summer students. Special thanks to Andy Silver and Sophia Konieczka, who truly put in the work maintaining cameras and reviewing thousands of images for me. I know a lot of those cameras were not fun to revisit, so thank you. In addition, I would like to thank Nick Luymes who was an amazing teacher and guide when it came to data analysis. Your weekly meetings answering all sorts of analysis questions and helping to develop R code was invaluable. I would likely never have gotten these models to completion without your help. Finally, thank you to Stephen Sucharzewski for being a fellow deer team grad student to brainstorm with and rope into helping with camera-trap fieldwork.

Lastly, I would like to thank my family and friends who have provided immense support during this thesis. To my parents, Greg and Leslie, who put me and my sisters' education above all else, instilling in us the importance of the pursuit of knowledge. I would not be where I am today without your examples of work ethic and your love. To my sisters, Emily and Jess, thank you for laying the groundwork as older sisters. You have been my greatest role models. And thank you for having the most adorable children who make me smile and remind me not to take life too seriously. Finally, a very special thanks to my partner, Drew. Your love, support, and coffee runs have carried me to the finish line. As a biologist and as my partner no one understands me or this project better. There is no one who I would rather talk about deer with.

Table of Contents

Abstract	ii
Acknowledgements	iv
List of Figures	vii
List of Tables	ix
Chapter 1: General Introduction.....	1
Research Questions.....	8
Chapter 2: Connecting white-tailed deer density and landscape effects using remote camera-traps in central Ontario	9
Introduction	9
Methods	17
<i>Study Area</i>	<i>17</i>
<i>Camera Trap Monitoring Design.....</i>	<i>20</i>
<i>Radio-collared Deer.....</i>	<i>21</i>
<i>Generalized Spatial Mark-Resight Model</i>	<i>23</i>
<i>Stage 1: Model of Marked Deer</i>	<i>24</i>
<i>Stage 2: Model of Unmarked Deer.....</i>	<i>26</i>
<i>Incorporating Covariates into the Model.....</i>	<i>28</i>
Results.....	31
<i>Capture and Resight Statistics</i>	<i>31</i>
<i>Stage 1 SCR for Detection Parameters.....</i>	<i>31</i>
<i>Stage 2 SCR for Deer Density and Abundance</i>	<i>32</i>
<i>Covariate Model.....</i>	<i>35</i>
Discussion.....	36
<i>Deer Density and Model Assessment.....</i>	<i>37</i>
<i>Factors Influencing Spatial Variation in Deer Density.....</i>	<i>40</i>
<i>Conclusion</i>	<i>45</i>
Chapter 3: Conclusion	46
References	53
Appendix.....	65

List of Figures

Figure 1. A) The distribution of chronic wasting disease in North America as of August, 2023 (National Wildlife Health Center and USGS, 2023). This map indicates states and provinces with positive cases both in free-ranging and captive cervid populations. B) Front cover of the Ontario Government 2019 Chronic Wasting Disease Prevention and Response Plan (OMNRF, 2019).9

Figure 2. Overview of the greater study area including the spatial scale boundary and Peterborough Crown Game Preserve boundary. Points indicate camera-trap locations within the camera study boundary in central Ontario, Canada. Includes roads and trails throughout the study area.....18

Figure 3. Example photo of radio-collared white-tailed deer with identifying placard (#07) captured by a camera-trap in central Ontario, Canada.22

Figure 4. Posterior mean estimates and 95% confidence intervals of σ , $\log\sigma$, λ_0 , $\log\lambda_0$ for ten, two-week primary periods (MM-DD) of collared deer in central Ontario. Month and day represent the start of the primary period. σ estimate was measured in meters and λ_0 was measured as a probability.32

Figure 5. Posterior mean estimates and 95% confidence intervals of abundance (N) and density (D) for ten two-week primary periods (MM-DD) of deer in central Ontario, Canada. Month and day represent the start of the primary period.33

Figure 6. Stage 2 percent coefficient of variation (CV) for the mean abundance of deer for each two-week primary period (MM-DD). Target CV in abundance estimates is $\leq 20\%$ indicated with dashed line. Combined CV for the 10 two-week periods was 55% when the standard deviation was 131 deer and the mean was 238 deer. Month and day represent the start of the primary period.34

Appendix

Figure A1. Visual representation of the Stage 1 telemetry points from the 39 radio-collared deer who were within the study area boundary, including the 2-km buffer, at least once during the 140-day study period. Each map represents the GPS points of the collared deer for each two-week primary period (MM-DD; first day of the primary

period). The pluses represent the camera-trap locations. If a deer was resighted by a camera-trap during the primary period it is denoted with the corresponding deer id color surrounding the camera-trap location. All camera-trap and GPS points are configured in UTM.....68

Figure A2. Stage 1 SCR models for all ten two-week primary periods (MM-DD) converged based on posterior σ samples from four chains of 15,000 iterations with corresponding Gelman-Rubin convergence statistic ($\hat{R} < 1.05$). Month and day represent the start of the primary period.69

Figure A3. Stage 1 SCR models for all ten two-week primary periods (MM-DD) converged based on posterior $\log\lambda_0$ samples from four chains of 15,000 iterations with corresponding Gelman-Rubin convergence statistic ($\hat{R} < 1.05$). Month and day represent the start of the primary period.69

Figure A4. Stage 2 SCR models for all ten two-week primary periods (MM-DD) converged based on posterior density (D) and abundance (N) samples from three chains of 22,500 iterations with corresponding Gelman-Rubin convergence statistic ($\hat{R} < 1.05$).....71

List of Tables

Table 1. Descriptive statistics of the spatial covariates incorporated in the model. Includes the mean, median, SD, minimum, and maximum percent of cell coverage for the 80 1-km ² cells used to estimate deer density.	29
Table 2. Stage 2 parameter summary statistics averaged across the 10 two-week primary periods including the mean, median, standard deviation (SD), 95% confidence intervals (CI) of parameter estimates.	34
Table 3. Covariate model results with magnitude of β parameter estimates, median, standard deviation (SD), 95% confidence intervals (CI) of spatial covariate effects on average deer density in Apsley, Ontario. Spatial covariates were standardized (mean = 0, sd= 1) meaning β parameter estimates predict the change in standard deviations of deer density with one standard deviation change of the corresponding covariate.	36
Appendix	
Table A1. Results of the MCP test and Wilcoxon signed-rank test comparing average male and female 95% MCP spaced used estimates for each two-week primary period. Month and day represent the start of the primary period.	65
Table A2. Stage 1 parameter summary statistics averaged across the 10 two-week primary periods including the mean, median, standard deviation (SD), 95% confidence intervals (CI) of parameter estimates.	70

Chapter 1: General Introduction

Human activities, from habitat loss and climate change to increased recreational activities in wild areas, are the primary threat to wildlife species and the ecological communities of which they are a part (Wong and Candolin, 2015; Reilly et al., 2017). These threats bring significant challenges for wildlife management and conservation. To maintain stable, healthy ecosystems, resource managers will need to have reliable information which might be improved with emerging techniques for monitoring and conservation (Hobbs et al., 2011). These techniques may take the form of increased surveillance for infectious diseases (Cardoso et al., 2022), modelling the effects of changing species distributions in response to a warming climate (Weiskopf et al., 2019), or quantifying the impacts of intentional and unintentional supplemental feeding of wildlife (Priesmeyer et al., 2012).

Emerging and expanding infectious diseases pose significant threats to wildlife species and are the focus of numerous management and research programs (Tompkins et al., 2015). One such disease in North America is Chronic Wasting Disease (CWD). CWD is a fatal prion disease that infects members of the Cervidae family (Rivera et al., 2019). First identified in captive mule deer (*Odocoileus hemionus*) at a wildlife facility in Colorado, USA, in 1967 (Williams and Young, 1980), it was later classified as a transmissible spongiform encephalopathy (TSE) disease in 1980. In 1981, CWD was first detected in wild free-ranging elk (*Cervus canadensis*) becoming the only known prion disease of wild free-ranging animals (Spraker et al., 1997; Williams and Miller, 2002). Since its discovery, CWD has spread across much of North America and has been

detected in either free-ranging or captive cervids in 30 states in the United States and four Canadian provinces (Figure 1. A; National Wildlife Health Center, 2023). CWD has also been reported in Norway, Finland, Sweden, and South Korea (Ågren et al., 2021). Species with confirmed positive cases of CWD include mule deer, elk, white-tailed deer (*Odocoileus virginianus*) (Spraker et al., 1997), moose (*Alces alces*) (Baeten et al., 2007), wild reindeer (*Ranifer tarandus*) (Benestad et al., 2016), and red deer (*Cervus elaphus*) (Vikøren et al., 2019). All species in the Cervidae family are probably susceptible to CWD and thus this disease poses a global threat to the health of cervids (Mawdsley, 2020).

CWD can be transmitted horizontally or vertically (Rivera et al., 2019). Horizontal transmission is likely the most common (Miller and Williams, 2003) with infection occurring due to direct contact with an infected individual or infected saliva, feces, or urine (Rivera et al., 2019). The infectious prion can also persist in the environment, specifically in the soil, resulting in infection via grazing and local persistence of the disease (Haley and Hoover, 2015). In areas where the disease has become endemic, it has yet to be eradicated and can have significant negative effects on populations, especially when combined with additional pressures like hunting (Edmunds et al., 2016). In Wyoming, DeVivo et al. (2017) estimated an annual rate of population decline of 21% given the current prevalence of CWD in the southeastern mule deer population [CWD prevalence 24%; 95% CI = 22%-27%] but estimated the population growth rate would be stable if CWD were eliminated as a cause of mortality. Further, the presence of CWD could reduce hunting activity, thereby leading to reductions in funding available to combat the disease. Thus, management agencies have primarily focused on trying to

prevent the entry of CWD into jurisdictions, to eradicate it to avoid CWD becoming endemic if there is a positive case, and ultimately to reduce the prevalence if it does become endemic (Rivera et al., 2019).

As of 2023, the province of Ontario has not detected a positive case of CWD but has a provincial surveillance program and response plan (Ontario Ministry of Natural Resources and Forestry [OMNRF], 2023). OMNRF has been testing wild cervids for CWD since 2002, as part of their *Chronic Wasting Disease Prevention and Response Plan* (Figure 1.B; OMNRF, 2019). This surveillance includes sampling from hunter-harvested and opportunistically sampled white-tailed deer, moose, and elk. With increasing cases of CWD in surrounding jurisdictions, it is a top priority of OMNRF to monitor high risk areas for positive cases to prevent the spread of CWD in the province (National Wildlife Health Center, 2020; OMNRF, 2019). In the event of a positive CWD case, the CWD response plan states that OMNRF will respond to determine the control zone and estimate the density of cervids within the control zone (OMNRF, 2019). After which, OMNRF will take several measures to reduce the spread and prevalence of CWD, including reducing the population (e.g., herd culling) of cervids in close proximity to infected animals. However, the response plan does not provide clear guidance for how OMNRF will determine the control zone and fails to consider the complexities of estimating cervid population densities. Consequently, my project provides guidance for estimating cervid density and factors influencing it using new technologies and statistical models.

Knowing how many cervids are on the landscape at any point of the year is critical for informing decisions for managing wildlife disease (Storm et al., 2013). However, estimating the density of animals is complex and the methods to do so are dependent on agency resources, environmental conditions, and study area scale (Burgar et al., 2018). Estimating cervid density has been an active area of research for decades (Forsyth et al., 2022), but recent improvements in technology and statistical modeling are allowing for a wider variety of estimation techniques. Recent advances include noninvasive genetic sampling through fecal DNA (Brazeal et al., 2017), aerial thermal imaging (Corcoran et al., 2021), and deploying infrared motion-activated camera traps (Parsons et al., 2017). Many of these technological advancements can be combined with innovative statistical models to improve the probability of detection and account for imperfect detection of cervids, especially in densely treed areas (Forsyth et al., 2022).

Of the technological advancements, camera-traps have become one of the primary tools for wildlife research and conservation (Glover-Kapfer et al., 2019). Camera-traps offer numerous advantages over other tools because they are non-invasive, non-discriminatory, cost-effective, can be placed for extended periods, and cover a variety of spatial scales (Burton et al., 2015). Camera-traps require image processing, which can be time consuming, but with advances in computer learning and image management, technology firms like Wildlife Insights and WildTrax are working to reduce processing times (Vélez et al., 2022; Wildlife Insights 2023; WildTrax 2023).

With the ubiquity of camera-trap studies, numerous statistical advancements have been made in recent years to address the variety of challenges that arise when

estimating population abundance and density. These statistical models vary depending on whether the population is composed of animals that are individually identifiable, partially-marked, or unmarked (Palencia et al., 2021). For species whose individuals are naturally identifiable, e.g., tigers (*Panthera tigris*), the preferred method includes using photos of individuals to build a capture-recapture model (Karanth, 1995). For partially-marked species, e.g., bucks with antlers, studies have used a spatially explicit capture-recapture model to estimate the abundance for a subset of individuals that are uniquely identifiable (Beaver et al., 2016), or have incorporated additional information like telemetry and radio-collared individuals to build a spatial mark-resight model (Margenau et al., 2022). However, many species are not uniquely identifiable or do not have a subset of the population marked, so other models have been developed, with mixed success, to estimate population density and abundance using camera-traps. Such models include spatial counts (Burgar et al., 2018), time to event models (Moeller et al., 2018), random encounter models (Rowcliffe et al., 2008), random encounter and staying time models (Nakashima et al., 2018), and distance sampling (Howe et al., 2017). Further statistical advancements include adding a spatial component to traditional capture-recapture models, allowing for direct estimates of density by modelling the population size over an explicit spatial region (Efford, 2004). These spatially explicit capture-recapture (SCR) models reveal how population densities are influenced by the surrounding landscape (Chandler and Royle, 2013). Many limitations exist for camera-trap studies (Burton et al., 2015); however, they represent a potentially attractive option for managers who need to estimate the density of wildlife populations or monitor a

population within a specific area. However, it is important to test these advancements prior to real-world deployment.

A cervid species of particular concern for wildlife managers as a driving force for CWD spread is white-tailed deer (Joly et al., 2003). With a reduction of natural predators, focused management practices, and adaptation to changing landscapes, white-tailed deer populations have grown rapidly in many parts of North America over the last half century (Garrott et al., 1993; VerCauteren et al., 2011). White-tailed deer are a generalist browser that moves between habitats, interacting with various other species, and they occur at high population densities across much of their range (Garrott et al., 1993). Deer are valued for their recreational and cultural significance, but they can also be controversial, especially in high densities, due to over-browsing and the hazard and cost of deer-vehicle collisions. Their complex social structures (matriarchal and bachelor groups) and seasonal movements (dispersal and winter aggregation) compound the risk of spreading CWD (Storm et al., 2013). For example, Oyer et al. (2007) recorded a 98 km dispersal from a yearling white-tailed female out of a CWD-endemic area, highlighting the risk for a large geographical spread of CWD.

The spread of CWD to new areas and affecting other sensitive cervid populations is exacerbated by climate change. As climate change accelerates, white-tailed deer are expected to expand their ranges further north (Dawe et al., 2014; Dawe and Boutin, 2016; Weiskopf, 2019), allowing them to move into areas previously uninhabited by deer. Increased anthropogenic changes (e.g., habitat fragmentation, road development, oil extraction) to the landscape are also likely to promote deer expansion (Darlington et

al., 2022). In addition, wildlife do not adhere to geo-political boundaries; therefore surveillance for CWD near states and provinces with known cases of CWD is imperative.

White-tailed deer winter aggregation is a concern for increasing the risk of CWD spreading (Cullingham, 2010). Near the northern limits of their distribution, white-tailed deer seasonally migrate between summer and winter areas to avoid heavy snows (Nelson, 1998). They tend to congregate in large numbers in wintering areas dominated by coniferous trees (Morrison et al., 2003). This high deer density increases the risk of direct contact between individuals and environmental contamination with CWD (Janousek et al., 2021), followed by large movements in the spring potentially leading to significant spread of disease over short time frames. Such effects might be exacerbated at winter supplemental feeding sites (Thompson et al., 2008). Unlike natural browse at wintering areas, which is spread out both vertically and horizontally, and does not get replaced after consumption, supplemental feeding sites increase deer concentration with repeated use of the sites. Many jurisdictions with CWD have banned supplemental feeding due to this risk (Sorensen et al., 2014). However, banning of supplemental feeding is often controversial among the public, many of whom rely on baiting to hunt and believe providing winter supplemental feed increases deer survival (Murray et al., 2016). Understanding where deer are and how they use resources, especially in winter, will be important in building foundational knowledge of deer ecology when preparing to respond to the potential occurrence of CWD.

One of the primary tools of population management of deer is hunting (Connelly et al., 2012). However, deer have developed predator avoidance strategies to reduce the

risk of harvest during the regulated hunting season. For example, deer may shift their activity patterns to avoid diurnal-only hunting (Little et al., 2016). Deer may also move to areas where hunting is restricted (e.g. game preserves, national parks, private properties; Rhoads et al., 2013). This has led to many of these refuges having unsustainably high deer densities, which, in turn, can lead to habitat degradation (Coffey and Johnston, 1997). Understanding the behavioral response of deer to predation risk will be important when evaluating potential management strategies to contain CWD.

Research Questions

Ontario has a large population of white-tailed deer whose range limits are likely to expand northward with climate change. There has not been a case of CWD detected in the province, but there have been positive cases in the surrounding jurisdictions (Figure 1. A; National Wildlife Health Center, 2023), and thus it is likely that CWD will eventually be detected in Ontario. The province currently has a CWD response plan in place that prescribes the rapid reduction of the local deer population around a positive case to prevent the disease from becoming endemic. Such an approach requires accurate and rapid population abundance and density estimation techniques. My thesis aimed to test a new method of estimating deer density in Ontario to give managers a potential tool to assess CWD control efforts. I used camera-traps and recently developed spatial-capture recapture models to address two primary questions:

1. Are camera-traps a viable option for short-term and long-term deployment to estimate density of white-tailed deer in Ontario?

2. Can spatial covariates be incorporated into a density model to evaluate how white-tailed deer use resources and identify areas of high local abundance?

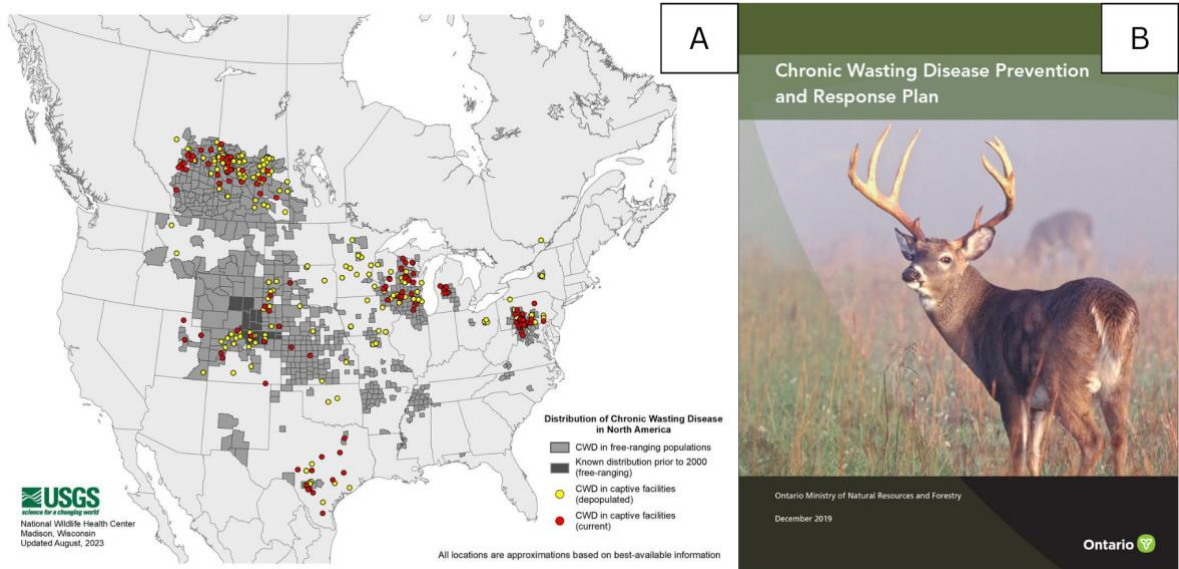


Figure 1. A) The distribution of chronic wasting disease in North America as of August, 2023 (National Wildlife Health Center and USGS, 2023). This map indicates states and provinces with positive cases both in free-ranging and captive cervid populations. B) Front cover of the Ontario Government 2019 Chronic Wasting Disease Prevention and Response Plan (OMNRF, 2019).

Chapter 2: Connecting white-tailed deer density and landscape effects using remote camera-traps in central Ontario

Introduction

Estimating population abundance is fundamental to understanding animal ecology and to managing and conserving wildlife (Pierce et al., 2012). Abundance estimates inform policy and management decisions, providing critical indicators of the status of wildlife populations. As a result, researchers continually innovate and refine technological and statistical techniques to improve understanding of the underlying drivers of population abundance (Royle et al., 2018). Advancements in these techniques

allow ecologists to make more informed management decisions, especially in the face of increasing environmental threats to wildlife populations.

Since the mid-20th century, biologists have used remote photography to document and monitor wildlife populations (O'Connell et al., 2011). As camera technologies advanced, the use of infrared motion-activated camera-traps has become an increasingly popular option for wildlife surveys (Burton et al., 2015). Modern camera-traps are small, can capture photos for up to a year, store thousands of photos, and require minimal maintenance once deployed (Locke et al., 2012). Camera-traps are advantageous relative to other methods because they can collect data for an extended period regardless of the time of day or season. The use of camera-traps also reduces bias induced by human presence, as researchers need to be present only during the deployment and maintenance of the cameras (Caravaggi et al., 2020). In addition, camera-traps are non-discriminatory and can capture information on several species simultaneously. The data collected from camera-traps can be used to answer fundamental ecological questions regarding species diversity (Oliver et al., 2023), resource use (Hofmann et al., 2016), individual behavior (Caravaggi et al., 2017), and population dynamics (Karanth et al., 2006), while being cost-effective and noninvasive (O'Connell et al., 2011). However, there are limitations with camera-traps including sensor performance, initial cost, and theft (Glover-Kapfer et al., 2019). Understanding these limitations allows biologists to develop more explicit methodologies to account for them (Burton et al., 2015). To ensure that inferences drawn from camera-trap data are reliable, testing study methods at varying scales and selecting appropriate statistical

analyses are imperative to further develop camera-traps as tools in wildlife conservation (Burton et al., 2015).

In addition to the advent of camera-traps, capture-recapture models serve as a foundational method for estimating population abundance. Capture-recapture methods were first developed in the early 1900's to monitor the annual change in the abundance of wildlife (Lincoln, 1930). Since then, capture-recapture models have further developed as computational power has increased and statistical methods have improved (Otis et al., 1978; Pollock, 1991; Bolger et al., 2012). The traditional approach to capture-recapture involves live trapping, marking, and releasing individuals, and creating capture histories through repeated sampling (Green et al., 2020). These individual capture histories and the related proportion of marked to unmarked individuals allow researchers to estimate the population size (Otis et al., 1978).

A limitation of such models is that they address only the numerator of density estimation (Green et al., 2020). The area (over which population density is calculated) is often delineated arbitrarily (Green et al., 2020; Royle et al., 2014). To address this limitation, researchers developed spatially explicit capture-recapture (SCR) models that explicitly incorporate the location of traps and estimate latent activity centers of captured animals, allowing for density to be estimated directly in the model without post-hoc calculations of the area (Borchers and Efford, 2008; Royle and Young, 2008). In this approach, density is estimated using a spatial point process to model the distribution of activity centers of individuals and estimate their capture probability as a function of the distance between the activity centers and trap locations (Royle et al.,

2014). This analysis assumes that individuals with activity centers closer to trap locations will be captured more often. Parameter estimates include λ_0 , which is the probability of capturing an individual at their activity center, and σ , which is the rate at which capture probability declines with distance measured in meters (Whittington et al., 2018). The sum of these activity centers represent the number of individuals in a population N across the defined state space S resulting in the estimated population density. By making the movement of individuals and trap locations explicit, researchers can incorporate spatial covariates into SCR models to quantify the effects of environmental factors on the distribution of activity centers and therefore population density (Royle et al., 2018). This allows researchers to connect population dynamics with landscape ecology to better understand the underlying processes influencing population densities (Linden et al., 2018; Proffitt et. al, 2015; Satter et al., 2019).

Nevertheless, a potentially major limitation of capture-recapture and SCR models is that individuals need to be marked or uniquely identifiable (Chandler and Royle, 2013). This is possible for genetic sampling studies (Goode et al., 2014), for camera-trap studies involving species with unique markings (Avgan et al., 2014), or for which a subset of the population is uniquely identifiable (Beaver et al., 2016). This need for individual identifiers limits the use of standard capture-recapture and SCR models for species which lack individual identification when camera-traps are the detectors. However, recent model extensions relax the requirement for individual identification, allowing for abundance and density estimation of unmarked or partially marked populations (Chandler and Royle, 2013; Whittington et al., 2018; Margenau et al., 2022). These

models include spatial count models (Chandler and Royle, 2013) and spatial mark-resight models (Whittington et al., 2018), which can be applied to camera-trap studies. To improve estimates, researchers recommend that any additional information regarding detection probability, such as encounter histories of individuals who are uniquely identifiable or ancillary spatial data gleaned from radiotelemetry, should be included in the model (Margenau et al., 2022).

Such additional information can be incorporated into spatial mark-resight (SMR) models. This innovative technique represents a cost-effective way to apply SCR techniques because only a portion of the population needs to be marked, either naturally or artificially (Whittington et al., 2018). For artificial marks, individuals are captured once, marked (e.g., by fitting a radio collar), and capture histories are built through resighting of these individuals. Camera-traps are often used as re-sighting detectors in these instances (Whittington et al., 2018). Recently Margenau et al. (2022) extended generalized SMR models to incorporate long-term data and applied them to estimate abundance of white-tailed deer in Florida, USA. They split the estimator into two stages to ease computational demands and allow flexibility with long-term monitoring efforts. In the first stage, they estimated detection parameters (σ, λ_0) using telemetry from radio-collared adult female deer and camera-trap detections of these animals. In the second stage, they estimated adult female density using camera-trap detections of females, treating all deer as unmarked and using the estimated detection parameters from stage one as priors in the second stage. In addition to easing computational demands, splitting the model into two stages allows for the second stage

of the model to be used independently if no concurrent telemetry data are available, provided appropriate detection priors can be incorporated into the model. Doing so results in a loss of some precision but allows for long-term monitoring without the need for continually marking individuals as long as researchers can assume consistent behavior across time.

Apart from the field and analytical procedures of population estimation, wildlife management often hinges on the precision and accuracy of the estimate. The accuracy of a population abundance estimate can rarely be determined since we do not know the true population size (Pierce et al., 2012). Instead, researchers can conduct simulation studies prior to field deployment to test the effect of different sampling scenarios on the accuracy of estimates (Kowalewski et al., 2015). Post-data collection accuracy can be inferred by comparing similar studies conducted within the study system. However, if a study area has never been previously sampled, researchers must rely on evaluating the precision of the estimates to determine their usefulness (Pierce et al., 2012). Precision is often evaluated by calculating the coefficient of variation (CV), which is the standard deviation of the estimate divided by the mean or the ratio of the sample variability to the abundance estimate, often reported as a percentage (Forsyth et al., 2022). The smaller the CV, the more precise and reliable the estimate. Wildlife managers generally strive for CVs of $\leq 20\%$ (Butler et al., 2020). However, researchers often fail to report measures of precision, especially CVs, making it difficult to compare the reliability of different sampling methods for wildlife management (Forsyth et al., 2022). By including

measurements of precision, researchers can better understand the effectiveness of survey methods.

White-tailed deer are an ideal study species to test the use of camera-traps and SMR model validity for estimating population density in Ontario, Canada. Deer are the most abundant of the province's four cervid species and are an important species ecologically, socially, and economically (OMNRF, 2017). They are also a concern as a major driver in the spread of chronic wasting disease (CWD; Joly et al., 2003). Accurately and precisely estimating the population size of deer, regardless of season, will be critical in Ontario's response to a positive CWD case (OMNRF, 2019). Deer also play an important ecological role in the systems they inhabit (Shelton et al., 2014). Deer are an important prey species for large carnivores, but in the absence of large carnivores they are often over-abundant leading to over-browsing and negative impacts on local plant understories (Flagel et al., 2015; Horsley et al., 2003; Rooney, 2009). On average there are 10,000 to 12,000 reported wildlife collisions in Ontario each year resulting in approximately 400 human injuries and \$800 million in damages with the majority of these collisions being with deer (Ontario Ministry of Transportation[OMT], 2018; OMT, 2020). Managing deer species to reduce the spread of CWD, the negative effects on plant communities, and vehicle collisions is difficult and requires a multi-pronged approach to address management objectives (McShea, 2012).

In addition to population size, understanding the local distribution of deer can be important to managing the species. Deer make decisions regarding trade-offs between increased predator risk (e.g., predation, hunter risk, vehicle collisions) and forage

availability (Dupke et al., 2017). This landscape of fear is not static; it varies spatially and temporally. Deer in areas with low natural predator risk, such as in suburban areas, will use the landscape differently and behave differently than those with high natural predator risk, such as in wilderness areas (Brown, 1999). Deer predation risks, including hunting risk, shift seasonally, which influences deer behavior and distribution (Cromsigt et al., 2013). Additionally, winter can be a particularly risky period for deer in the northern extent of their range as deep snow increases canid predation (Olson et al., 2021; Rieucou et al., 2007). Understanding deer responses to presumed predation risk and why they use certain areas more than others is fundamental to managing the species.

The scale is an important consideration when estimating abundance and examining the influence of environmental effects that vary spatially on species (Bissonette, 2012; McDonald et al., 2012). Much of the knowledge on variation in deer use of landscapes comes from studying individual behavior through direct observations or radio-telemetry (Little et al., 2016) (Darlington et al., 2022). The results of these studies are often extrapolated to entire populations, possibly introducing bias or uncertainty and potentially obscuring population-level patterns, which are most important for management decision making. By contrast, there is also a risk in studying these processes at too coarse a scale. If researchers make inferences across large-spatial scales they might miss important nuances, or be unable to resolve influential spatial effects (McDonald et al., 2012). Instead, when population-level studies that link density and spatial environmental factors can be conducted at a fine scale for a local population,

managers can make decisions that are directly informed by the deer population they manage (Royle et al., 2018). This might include decisions regarding harvest quotas, conservation of critical over-winter areas, or road and trail development. By modeling the influence of landscape factors on deer density and making specific habitat-related management decisions, managers can better evaluate the effectiveness of these management decisions.

Here, we assess a recently developed spatial-mark resight model for estimating white-tailed deer density and abundance in Ontario. Specifically, using camera-traps, we were interested in whether the model provided feasible and precise density estimates. To assess the influence of spatial environmental factors on deer density, we incorporated spatial covariates, which have not been tested for this SMR model. Our research objectives were two-fold. First, we used telemetry and camera-trap data to build a SMR model to estimate the abundance of a local deer population. Second, we built upon this model by incorporating landscape covariates to assess the effect of environmental factors on fine-scale variations in deer density.

Methods

Study Area

This study was conducted within a 16-km² area near Apsley, Ontario, Canada (Figure 2). This area, part of provincial Wildlife Management Unit 60 (OMNRF, 2021), was divided into two adjacent study sites with differing deer management strategies. The northern portion of the study area was public land (approximately 6 km²) that allowed for hunting and trapping. The southern portion of the study area was part of the

Peterborough Crown Game Preserve (approximately 10 km²). The northern area was open to bow hunters from October 1st to December 15th 2021 and firearm hunters November 1st to November 14th 2021 (OMNRF, 2021). Except for local Indigenous communities, hunting and trapping was prohibited in the Game Preserve (OMNR, 1977). However, other recreational activities were allowed in both areas including snowmobiling, off-road vehicle use, cross-country skiing, and hiking. The study area was surrounded by private property, with a network of residential and logging roads throughout the area.

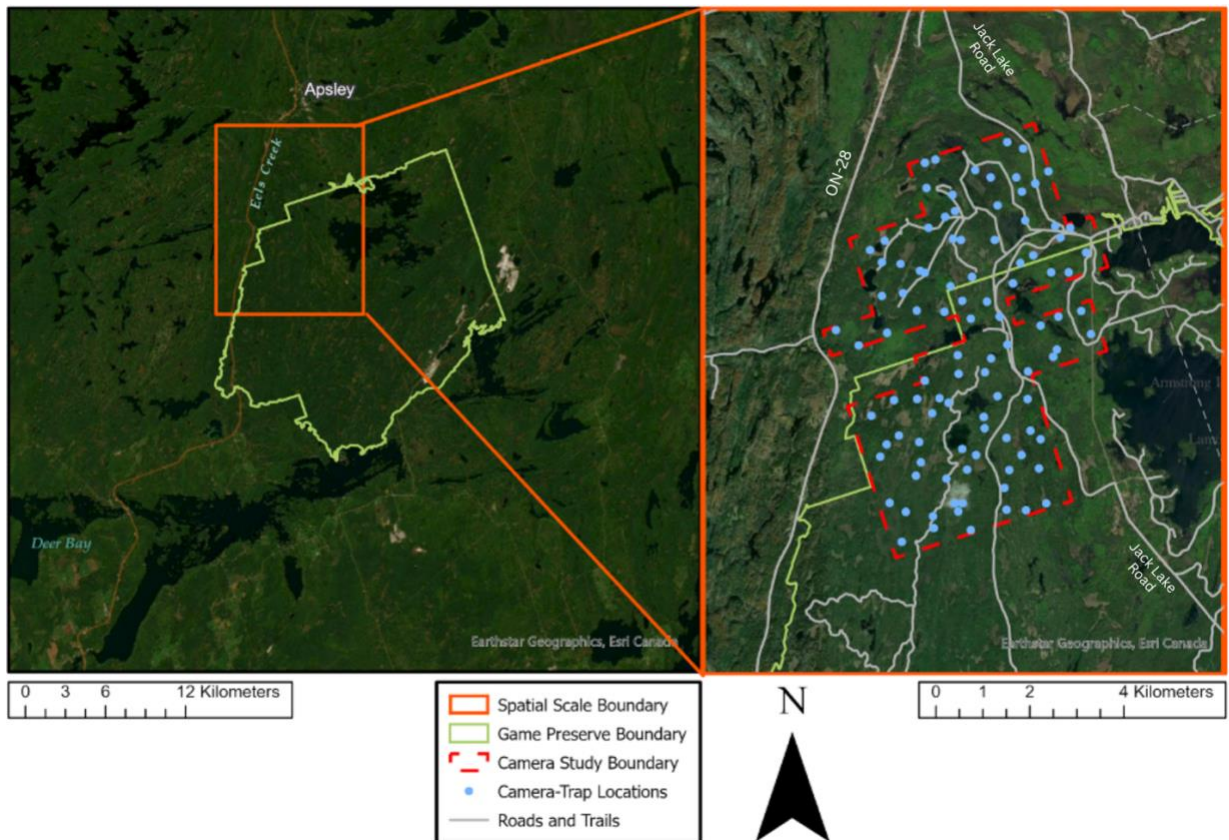


Figure 2. Overview of the greater study area including the spatial scale boundary and Peterborough Crown Game Preserve boundary. Points indicate camera-trap locations within the camera study boundary in central Ontario, Canada. Includes roads and trails throughout the study area.

The study area fell within the Great Lakes-St. Lawrence Forest Region (Rowe, 1972), and within the Bancroft-Minden Forest Management Unit (OMNRF, 2020a). The area was predominantly a mixed conifer-deciduous forest. The primary tree species includes white pine (*Pinus strobus*), sugar maple (*Acer saccharum*), eastern white cedar (*Thuja occidentalis*), red pine (*Pinus resinosa*), red maple (*Acer rubrum*), white oak (*Quercus alba.*), red oak (*Quercus rubra*), and balsam fir (*Abies balsamea*) (OMNRF, 2020b). The climate was humid-continental, consisting of mild springs and autumns, cold winters, and hot summers (Peel et al., 2007). Monthly average temperature for the area ranged from -5.1°C in January 2022 to 27.1°C in July 2022 (Environment and Climate Change Canada, 2022).

The study area was located in Peterborough County, specifically in North Kawartha Township which had a population of 2,877 (3.9 people/km²) in 2021 (Statistics Canada, 2021). This included 3,693 private residences, of which 1,364 were occupied year-round. In addition to the study species, other common large mammals were American black bear (*Ursus americanus*) and moose (*Alces alces*). Canids included red fox (*Vulpes vulpes*) and eastern coyote (*Canis latrans var*). Smaller mammals consisted of fisher (*Pekania pennanti*), American marten (*Martes americana*), American mink (*Neovision vision*), snowshoe hare (*Lepus americanus*), northern raccoon (*Procyon lotor*), North American porcupine (*Erethizon dorsatum*), and several squirrel species (Sciuridae family).

Camera Trap Monitoring Design

OMNRF staff and I deployed 100 infrared-motion activated camera-traps, set to operate continuously, beginning March 10th 2021 to May 21st 2022. Cameras included 69 Reconyx UltraFire XP9 and 31 Reconyx HyperFire HC600 (Reconyx Inc., Holmen, WI, USA), with models distributed throughout the study area. Camera settings included 3 pictures per trigger, 0 second delay between triggers, trigger sensitivity set to high, and flash active for nighttime triggers. Timelapse photos were taken at 12 pm each day to ensure the camera was functioning and the camera view was unobstructed. A sampling occasion was defined as a day that the camera was active for 24 consecutive hours with no malfunctions or visibility concerns preventing detection and identification of species triggering the camera. If all cameras were active and unobstructed then one day provided 100 sampling occasions.

We deployed the cameras using a stratified random design. A 16-hectare grid was overlaid across the study area resulting in one-hundred 400 m x 400 m cells for camera deployment, with 40 cells in the public land and 60 cells in the game preserve. Within each cell, a single camera was placed within 30 m of a randomly generated point. The points were randomly generated before the camera deployments using the geospatial software ArcGIS Pro 2.7.0 (ESRI, Redlands, CA, USA). Cameras were deployed to maximize detections of deer, including facing game trails. If there was not a suitable place to set up the camera within 30 m of the randomized point due to land cover types lacking trees for camera attachment, specifically open fields or bodies of water, we set the camera on the edge of the open area (Beaver et al., 2016). Cameras were placed

approximately 1 m off the ground to avoid visual obstruction by snow and facing north to avoid sun obstruction. We revisited the cameras every 3 to 4 months to replace the SD card, check the battery level, and ensure each camera was functioning. Photos were processed and uploaded to Wildlife Insights (Wildlife Insights, 2023). All photos were reviewed by trained personnel for species identification, number of individuals present, sex identification when possible, age classification when possible, and individual identification for radio-collared deer.

Although the cameras were active from March 10th 2021 to May 21st 2022, for this study, I used a sub-sample of the camera data to coincide with the deployment of GPS radio-collars on deer within the study area. Specifically, I used data from January 1st 2022 to May 20th 2022 for a total of 140 days and 13,190 sampling occasions.

Radio-collared Deer

From December 2021 through March 2022, deer were captured using Clover traps (Clover, 1956) baited with a small amount of corn. We followed animal handling and care protocols approved by the Ontario Ministry of Natural Resources and Forestry and the Trent University Animal Care Ethics committees with guidelines set by the Canadian Council on Animal Care (OMNRF and Trent University permit #22-460). Capture protocols also followed the guidelines of the American Society of Mammalogists (Sikes et al., 2019). Captures were non-discriminatory, resulting in the capture of both sexes and deer of varying age classes (adult, yearling, fawn). Every captured deer that was deemed to be in sufficient condition to wear a collar was fitted with a Lotek LiteTrack Iridium 420 global positioning system (GPS) collar (Lotek Wireless Inc,

Newmarket, ON) programmed to send one GPS location every 2 hours via satellite to the online Lotek Web Service. Magnetic expanders were added to the collars deployed on males to accommodate neck growth during the rutting season. Collars were equipped with a timed drop-off mechanism that could be remotely triggered if needed. Collars were fit with a rubber gasket that would degrade over time to ensure collars dropped in the event of a drop-off failure. Unique ID placards were added to both sides of all the collars (Figure 3). These placards, in addition to GPS movements, allowed for identification of radio-collared individuals in camera-trap photos. GPS-telemetry locations collected within one-week post-capture were not included due to potential atypical movements related to capture.



Figure 3. Example photo of radio-collared white-tailed deer with identifying placard (#07) captured by a camera-trap in central Ontario, Canada.

Generalized Spatial Mark-Resight Model

I used the generalized spatial-mark resight model developed by Margenau et al. (2022) to estimate density (number deer/ km²) and abundance (population size) of deer in the study area. This model consisted of two stages which reduced the computational demands of hierarchical modeling, while still using recursive Bayesian inference to fit spatial capture-recapture (SCR) models. In the first stage, telemetry data and camera detections of collared deer were used to estimate the detection parameters (λ_0, σ) using a SCR model. The encounter rate, λ_0 , represented the probability of detecting an individual if the distance (d_i) from the activity center (s_i) of the individual to a camera location (x_j) was zero. The spatial scale parameter, σ (measured in meters), was the rate at which the detection probability of an individual decreases as a function of Euclidean distance between the camera and activity center. In the second stage, these estimated detection parameters were used as priors to estimate density and abundance, with all deer treated as unmarked using an unmarked SCR model. Density was allowed to vary across two-week sampling periods, but a first-order autoregressive (AR[1]) time-series model was included in both stages to account for autocorrelation in detection and density.

The models were broken into consecutive primary periods $t = 1, \dots, T$, each consisting of 2 weeks during which I considered the deer population to be closed (i.e. limited deaths and dispersal). Each primary period was then broken into 14 secondary periods k . The 78.93-km² state space S included the 16-km² camera array and a 2-km rectangular buffer. The buffer ensured that individuals with activity centers outside the

state space or near the edge of the space had a near-zero probability of being detected at cameras and was based on the maximum σ value across sampling periods.

I did not differentiate between male and females when estimating detection parameters and assumed that there are no differences in movements between the sexes. To help validate this assumption I estimated each deer's home range using a minimum convex polygon (MCP, 95% confidence area) during each two-week primary period. I then conducted a Wilcoxon signed-rank test comparing the average home ranges of radio-collared males and females to ensure they were not significantly different from one another. The alpha value (α) was adjusted using a Bonferroni correction (α/n) to avoid type I errors when running the ten Wilcoxon signed-rank tests. The alpha was adjusted from $\alpha= 0.05$ to $\alpha=0.005$ ($\alpha= 0.05/10$).

Stage 1: Model of Marked Deer

In the first stage of the model fitting, I used the telemetry locations and the detection histories of marked individuals to estimate detection parameters for each primary period. I only used the GPS-telemetry locations of deer that were within the camera grid or the surrounding rectangular buffer (2 km) at some point during the 140-day sampling period (Figure A1). The telemetry locations informed the model on the activity centers of the marked individuals, while the detection histories of marked individuals provided information on the probability of detection. The activity center for marked individual, i , during primary period, t , was assumed to be distributed uniformly: $s_{it} \sim Uniform(S)$, where S was the spatial domain of the study area plus the 2 km buffer. The telemetry locations of individual, i , during primary period, t , and secondary

period, k , were modeled using a bivariate normal distribution with the latent activity center as the mean: $u_{ikt} \sim Normal(s_{it}, \sigma^2 I)$. The expected number of detections (λ_{ijkt}) of a marked individual i at camera j on secondary sampling period k and during primary period t was assumed to decrease with Euclidean distance (d_{ijt}) between the activity center and the cameras. To estimate the expected number of detections at each camera, I used a common encounter rate function $\lambda_{ijkt} = \lambda_{0,t} e^{-\frac{d_{ijt}^2}{2\sigma_t^2}}$ which allowed the probability of detection to decrease as a function of distance of the camera from the activity center. The individual-level encounter histories of the marked deer were modeled with a Bernoulli distribution. For each secondary period I used a binary detection (1) or non-detection (0) of marked individuals at cameras:

$y_{ijkt} \sim Bernoulli(1 - e^{-\lambda_{ijkt} z_{it}})$. A first-order autoregressive (AR[1]) process model on the detection parameters was used to allow for temporal variation between primary periods with a logarithmic link to account for temporal autocorrelation:

$$f(D_t) = X_t' \beta_t + \epsilon_t$$

$$\epsilon_t \sim Normal(\alpha \epsilon_{t-1}, \tau^2)$$

where $f()$ was the link function, X_t was a vector of covariates, β_t was a vector of coefficients, ϵ_t was the error term, α was the autocorrelation parameter, and τ^2 was the variance of the error terms.

In the second stage of the model fitting, I used the joint posterior distribution for $\lambda_{0,t}$ and σ_t samples from the first stage. I fit the first stage of the model using STAN from the package *rstan* (Stan Development Team, 2023) in the R statistical software (R Core Team, 2022). I made inference using 60,000 posterior samples from four Markov chains

after a burn-in of 15,000 iterations. I checked convergence of the posterior samples using visual inspection of the MCMC chains and using the Gelman-Rubin convergence statistic (\hat{R}), with $\hat{R} < 1.1$ indicative of convergence (Brooks and Gelman, 1998).

Stage 2: Model of Unmarked Deer

By treating all deer as unmarked in the second stage, this modelling approach avoided the need to model different spatial distributions of marked and unmarked individuals. In addition, since the marked individuals were presumably a random subset of the population, I assumed they had similar spatial distributions as unmarked individuals. These assumptions help avoid the biased inferences that can arise when combining data on marked and unmarked individuals, when differences in spatial distributions are not taken into consideration (Margenau et al., 2022).

I used the estimated posteriors of $\lambda_{0,t}$ and σ^t from stage one for each primary time period to inform the prior multivariate normal distribution in stage two. This allowed for more precise estimates of the detection parameters for the stage two unmarked SCR model. Similar to the first stage, an AR[1] model was used to account for temporal variation in density and abundance between primary periods with an identity link that ensured density was strictly positive.

Instead of putting a prior directly on abundance (N_t), I used a data augmentation approach that specified an augmented population size during each primary period, M_t that fixed the dimensions of the parameter space. The augmented population size must be larger than the possible abundance ($M_t \gg N_t$) (Margenau et al., 2022). Abundance

was modeled as $N_t = \sum_{i=1}^{M_t} z_{it}$ with $z_{it} \sim \text{Bernoulli}(\psi_t)$ and $\psi_t = \frac{E(N_t)}{M_t} = \frac{D_t A}{M_t}$, with A

being the area of the region within which N_t individuals occur. The latent variable z_{it} indicated whether an individual of the augmented population was an actual member in the study population. The implication of this model was that the marginal distribution of abundance is $N_t \sim \text{Binomial}(M_t, \psi_t)$, which because M_t was large, was equivalent to a Poisson assumption used in point process models.

Density was assumed to be spatially uniform. This allowed for each individual's spatial distribution to be modeled as $s_{it} \sim \text{Uniform}(S)$, where s_{it} was an individual's activity center within the two-dimensional spatial region S . The expected number of detections of each individual (λ_{ijkt}) was modeled with the same encounter rate function as in stage one. However, because not all deer were uniquely identifiable, I used binary counts if at least one deer was detected (1) or not-detected (0) at each camera on each secondary sampling occasion instead of using a Bernoulli distribution to model the individual-level encounter as per stage one. It was assumed that the number of independent detections of each individual was Poisson distributed with the model of the binary data specified as: $n_{jkt} \sim \text{Bernoulli}(1 - e^{-\Lambda_{jkt}})$ where $\Lambda_{jkt} = \sum_{i=1}^{M_t} \lambda_{ijkt} z_{it}$. I fit the second stage of the model using the *Nimble* package in R (de Valpine et al., 2017; R Core Team, 2022). I made inferences using 67,500 posterior samples from three Markov chains after a burn-in of 5,000 iterations and a thinning rate of 2. I checked convergence of the posterior samples using visual inspection of the MCMC chains and using the Gelman-Rubin convergence statistic, with values $\hat{R} < 1.1$ indicative of convergence (Brooks and Gelman, 1998). Additionally I calculated the coefficient of variation (CV) for each primary period and the entire study period. CV was calculated as the $\frac{SD}{mean} * 100$.

Incorporating Covariates into the Model

Next, I ran a model to understand how spatial covariates influenced deer density. Again, I used the posterior distributions of $\lambda_{0,t}$ and σ^t from stage one as priors in the covariate model. However, instead of estimating density across the entire area, I estimated the density within 80 1-km² cells that overlapped the state space. These smaller units were chosen to match the space use size of individual deer to approximate the area and ecological features to which a deer respond. The same model used in stage two was applied to each grid cell with an additional equation to account for spatial effects on density. This equation $ED_{gt} = ED_t + \beta_1 X_1 + \beta_2 X_2 + \dots \beta_n X_n$ represented the estimated deer density of grid cell g at primary period t as a function of the estimated density during that primary period and a n number of covariates X_n with a vector of regression coefficients β_n . With the additional spatial covariates, the latent variable z_{igt} indicated whether an individual was a member of the population and had an activity center within that grid cell. This allowed me to model deviations of average density of the study area across all the time periods based on these spatial covariates.

Eight spatial covariates were chosen and summarized for each 1 km² cell (Table 1). These included hunted area (private and public land where licensed hunting is allowed), protected area (Peterborough Crown Game Preserve), mixed forest, coniferous forest, deciduous forest, grassland, water, and road and trail density. The percent of cell coverage for each covariate was determined using the ArcGIS Pro V 2.7.0 zonal statistics tool (Esri, Redlands, CA, USA) for each covariate data source. Each covariate was standardized (to mean of 0 and standard deviation of 1) prior to inclusion

in the model to allow me to compare effect sizes. This also helped with model convergence.

Table 1. Descriptive statistics of the spatial covariates incorporated in the model. Includes the mean, median, SD, minimum, and maximum percent of cell coverage for the 80 1-km² cells used to estimate deer density.

Spatial Covariate	Mean	Median	SD	Min	Max
Hunted Area	0.63	0.95	0.42	0.00	1.00
Protected Area	0.45	0.15	0.47	0.00	1.00
Mixed Forest	0.47	0.50	0.18	0.02	0.79
Coniferous Forest	0.25	0.17	0.23	0.00	0.96
Deciduous Forest	0.13	0.08	0.14	0.00	0.55
Grassland	0.01	0.01	0.02	0.00	0.16
Water	0.10	0.04	0.19	0.00	0.95
Road and Trail Density (km/km ²)	1.07	1.03	0.98	0.00	4.12

To assess the impact of hunting regulation type on deer density, I used the Crown Game Preserves layer from Land Information Ontario to map the Peterborough Crown Game Preserve polygon. I assumed licensed hunting was allowed on all land outside the game preserve. I considered the land area within the game preserve to be a refuge for deer and determined the percent of hunting regulation type (hunted vs protected) for each cell.

To assess the effect of landcover type on deer density, I used landcover classes at 30m resolution from the North American Land Cover dataset based on 2020 Landsat satellite imagery (NALCMS, 2023). Five landcover classes were selected (mixed forest, coniferous forest, deciduous forest, grassland, and water) based on their potential

importance to deer, especially during winter (DelGiudice et al., 2013), and their relative abundance on the landscape. I created separate layers for each landcover class. To do this I coded the focal layer as 1 and all other landcover types as 0. This allowed me to use the zonal statistics tool in ArcGIS Pro to calculate the percentage of area covered in each cell by each landcover class.

The final covariate included in the model was road and trail density. These data were obtained from the Canada National Road Network dataset (Statistics Canada, 2022), Ontario Trail Network dataset (OMNRF, 2022), and field observations of GPS tracks of ATV and snowmobile trails. Highways, roads, and trails were combined into one layer to assess influence of human created linear features on deer density. The road density (km/km^2) was determined by calculating the sum length of road and trails within each cell and dividing it by the total area of the cell.

I examined pairwise correlations between all covariates and removed highly correlated covariates from the same model when $|r| > 0.7$ (Dormann et al., 2013). I fit the SMR covariate model using the *Nimble* package in R (de Valpine et al., 2017; R Core Team, 2022). I made inference using 67,500 posterior samples from three Markov chains after a burn-in of 5,000 iterations and a thinning rate of 2. I checked convergence of the posterior samples using visual inspection of the MCMC chains and using the Gelman-Rubin convergence statistic, with $\hat{R} < 1.1$ indicative of convergence (Brooks and Gelman, 1998).

Results

Capture and Resight Statistics

During the 140-day sampling period, camera-traps recorded 40,619 photos, of which 23,010 photos contained deer representing 1,069 unique detections. We captured and radio-collared 84 deer between December 2021 to March 2022. This included 58 females (29 adults, 7 yearlings, 22 fawns) and 26 males (13 adults, 1 yearling, 12 fawns). Of the 84 deer captured we used telemetry locations and capture histories of 39 deer who were within the study area boundary at some point during the study, resulting in the analysis of 18,336 GPS-telemetry locations. The 39 deer included 27 females (17 adults, 2 yearlings, 8 fawns) and 12 males (7 adults, 5 fawns). Of the 39 individual deer with GPS locations within our study boundary, 19 were re-sighted by a camera trap on 89 occasions. The average area used by these marked individuals during the study period was 7.65 km² (95% CI= 0.21, 59.14; SD= 16.43) and 7.14 km² (95% CI= 0.05, 57.71; SD= 21.02) for males and females, respectively. Using the Bonferroni adjusted alpha level of 0.005, there was no significant difference ($p \leq 0.005$) in the area used of female and male deer during the 10 two-week study periods (Table A1).

Stage 1 SCR for Detection Parameters

The stage one model successfully converged based on the visual inspection of the MCMC chains of posterior samples of the spatial scale parameter σ and the encounter rate $\log\lambda_0$ with the $\hat{R} < 1.05$ for each primary period (Figure A2, Figure A3). The mean spatial scale parameter (σ) for the 140-day sampling period was 469.74 m (95% CI= 261.80 m, 841.83 m; SD= 169.63 m; Figure 4). The mean baseline encounter probability

(λ_0) for the 140-day sampling period was $3.35e^{-04}$ (95% CI= $3.98e^{-08}$, 0.0026; SD= $7.45e^{-04}$; Figure 4). Estimates of σ varied due to seasonal movement of deer, reaching a peak during the fifth primary period (02-26 to 03-11). Estimates of λ_0 were low due to the small sample size of resights relative to the number of sampling occasions. Additional model parameter summary statistics can be found in the appendix (Table A2).

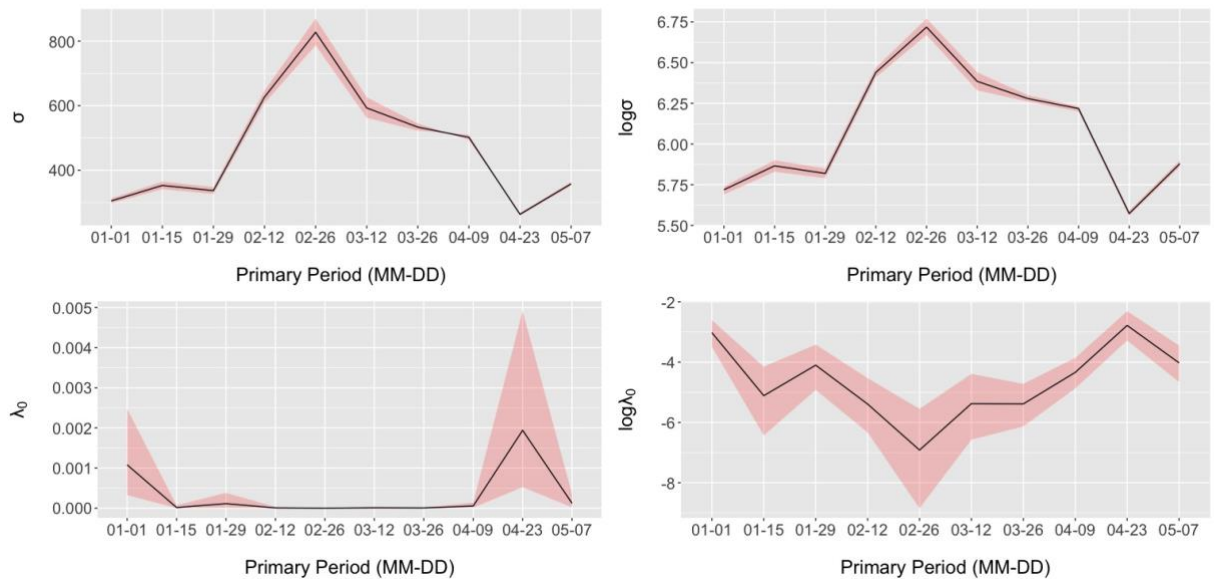


Figure 4. Posterior mean estimates and 95% confidence intervals of σ , $\log\sigma$, λ_0 , $\log\lambda_0$ for ten, two-week primary periods (MM-DD) of collared deer in central Ontario. Month and day represent the start of the primary period. σ estimate was measured in meters and λ_0 was measured as a probability.

Stage 2 SCR for Deer Density and Abundance

The stage two model successfully converged based on the visual inspection of the MCMC chains of posterior samples of the density (D) and abundance (N) estimates with the \hat{R} value for each primary period <1.05 (Figure A4). The mean deer density during the study period was 3.0 deer/km² (95% CI= 0.1, 5.8; SD= 1.7; CV= 55%) with a mean abundance of 238 deer (95% CI=10, 460; SD= 131; CV= 55%). There was a large fluctuation in density and abundance during the study period between individual

fortnights (Figure 5). The lowest mean density was 0.2 deer/km² (95% CI= 0.1, 0.4; SD= 0.1; CV= 50%) during the fifth primary period (02-26 to 03-11) with an abundance estimate of 15 deer (95% CI= 6, 32; SD= 7; CV= 47%). The highest mean density was 4.8 deer/km² (95% CI= 3.1, 6.2; SD= 0.8; CV= 17%) during the tenth primary period (05-07 to 05-20) with an abundance estimate of 378 deer (95% CI= 244, 490; SD= 66; CV= 17%). The coefficient of variation (CV) varied considerably during the study with four primary periods where CV ≤ 20% (the target for survey precision) and six primary periods where CV > 20% (Figure 6). The autocorrelation for density estimates was $\alpha = 0.59$ (Table 2). There was a small positive temporal population trend ($\beta_1 = 0.013$; Table 2) with a posterior probability of 0.56 that the trend was positive during the study period.

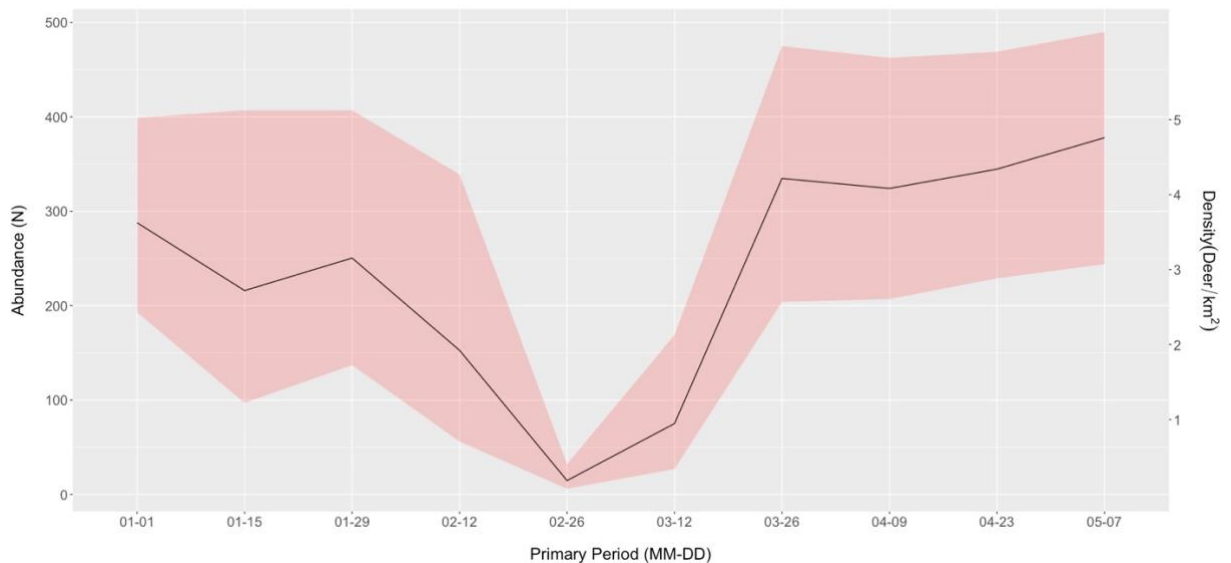


Figure 5. Posterior mean estimates and 95% confidence intervals of abundance (N) and density (D) for ten two-week primary periods (MM-DD) of deer in central Ontario, Canada. Month and day represent the start of the primary period.

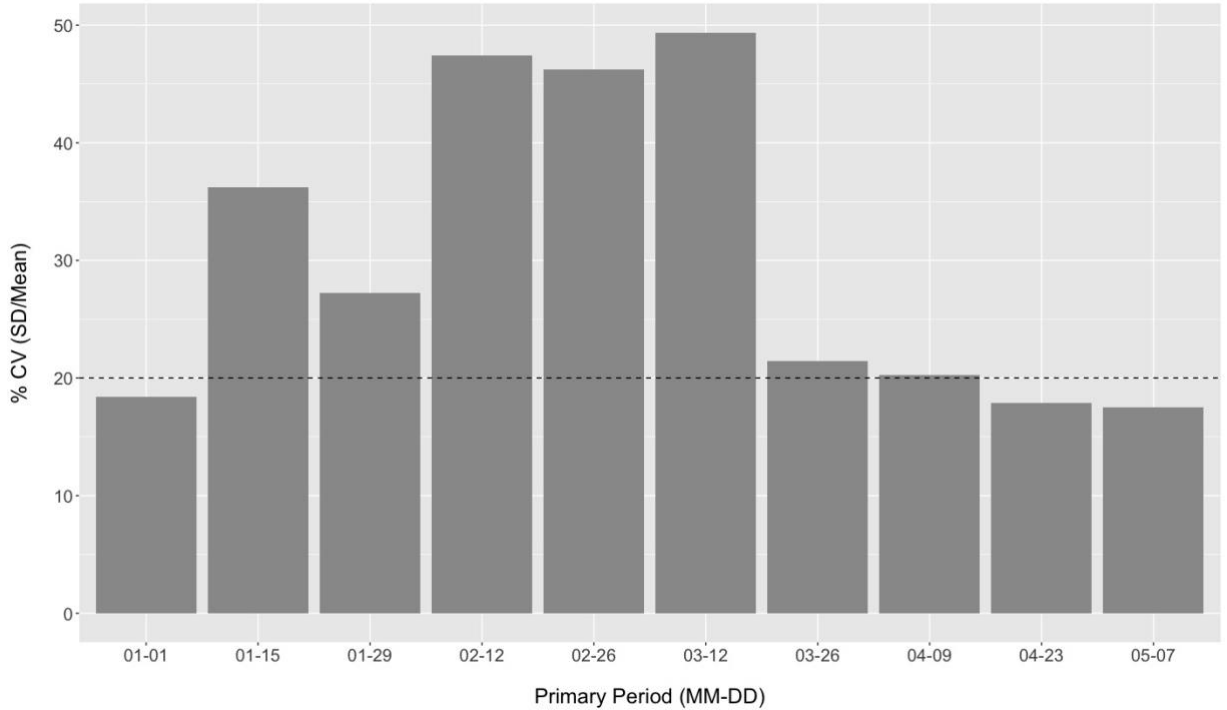


Figure 6. Stage 2 percent coefficient of variation (CV) for the mean abundance of deer for each two-week primary period (MM-DD). Target CV in abundance estimates is $\leq 20\%$ indicated with dashed line. Combined CV for the 10 two-week periods was 55% when the standard deviation was 131 deer and the mean was 238 deer. Month and day represent the start of the primary period.

Table 2. Stage 2 parameter summary statistics averaged across the 10 two-week primary periods including the mean, median, standard deviation (SD), 95% confidence intervals (CI) of parameter estimates.

Stage 2 Parameter	Mean	Median	SD	Lower CI	Upper CI
α	0.59	0.65	0.30	-0.15	0.98
β_0	3.80	3.80	1.18	1.35	6.11
β_1	0.013	0.014	0.092	-0.172	0.188
ϵ_{SD}	1.53	1.55	0.28	0.96	1.97
$\bar{\sigma}$	467.02	429.37	166.4	261.72	828.01
$\bar{\lambda}_0$	0.04	0.03	0.03	0.01	0.10

Covariate Model

Three of the six spatial covariates had a significant effect on average deer density in the study area. Mixed forest, deciduous forest, and road and trails had significant negative influences on the average deer density (Table 3). On average, for every 10% increase in mixed forest percentage there was a 0.12 (deer/km²) decrease in deer density. Similarly, on average for every 10% increase in deciduous forest there was a 0.14 (deer/km²) decrease in deer density. The coniferous landcover covariate was not included in the model, but instead used as the reference covariate due to high collinearity with the mixed forest landcover ($|r|=0.77$). Finally, on average for every 1 km/km² increase in road and trail density there was a 0.21 (deer/km²) decrease in deer density. The difference between the three significant β estimates was not statistically significant and they appear to influence deer density equally (Table 3).

The game preserve had a positive influence on average deer density, but the 95% confidence intervals overlapped zero (Table 3). However, there was a posterior probability of 0.95 that the game preserve had a positive influence on deer density. There was an average 9% (95% CI= 4%, 22%; SD= 6%) increase of deer density inside the game preserve compared to outside the game preserve during the study period. Presence of grassland had a non-significant positive influence on deer density and water had a non-significant negative influence on deer density (Table 3).

Table 3. Covariate model results with magnitude of β parameter estimates, median, standard deviation (SD), 95% confidence intervals (CI) of spatial covariate effects on average deer density in Apsley, Ontario. Spatial covariates were standardized (mean = 0, sd= 1) meaning β parameter estimates predict the change in standard deviations of deer density with one standard deviation change of the corresponding covariate.

Spatial Covariate	β Estimate	Median	SD	Lower CI	Upper CI
Game Preserve	0.1160	0.1160	0.0702	-0.0205	0.2550
Mixed Forest	-0.2130	-0.2130	0.0733	-0.3590	-0.0698
Deciduous Forest	-0.1920	-0.1920	0.0828	-0.3580	-0.0317
Grassland	0.0762	0.0767	0.0938	-0.1070	0.2590
Water	-0.0975	-0.0984	0.0871	-0.2650	0.0744
Road and Trails	-0.20270	-0.2070	0.0807	-0.3660	-0.0495

Note: Bold text indicates β estimates with significant effects (95% confidence intervals do not include 0).

Discussion

Quantifying population abundance and understanding how animals are distributed on the landscape are integral to the ecological study and management of wildlife populations (Herrando-Pérez et al., 2012). We used a recently developed, two-stage SMR model to estimate abundance of a partially marked population of white-tailed deer in central Ontario. Furthermore, we modified the model to incorporate spatial covariates, which allowed us to assess what environmental factors influenced variation in deer density at a fine resolution. The results revealed temporal dynamics in abundance, while indicating deer avoidance of mixed and deciduous forests during winter and our approach provides a framework for wildlife managers to estimate population abundance of deer using camera-traps.

Specifically, our stage two estimates captured temporal changes in abundance due to seasonal fluctuations in the number of deer in the study area as deer migrated to and from winter deer-yards (Figure 5). The results of our spatial covariate model indicate that deer in the area occurred at higher densities in coniferous forests, with mixed forest and deciduous forest having lower deer density (Table 3). The density of deer in the protected game preserve was marginally higher than outside the game preserve, but not significantly. In addition, deer preferred areas with lower road and trail density.

Deer Density and Model Assessment

Despite occupying much of North America and expanding their range northward, white-tailed deer densities can vary widely based on local conditions. As habitat generalists, deer occupy a variety of habitats, but some habitats and conditions are more suitable, leading to high densities and localized overabundance (Vercauteren et al., 2011). Deer densities can be particularly high in suburban and exurban areas due to the patchwork landscape types, including a mixture of forest, residential, and farmland (Lovely et al., 2013). These areas often have fewer natural predators and hunters resulting in deer densities up to 80 deer/km², in stark contrast to the target densities in many jurisdictions of <10 deer/km² (Williams et al., 2013). On the other hand, areas with less human development, higher hunter participation, and more predators tend to have lower deer populations. For example, deer density in areas of northern Michigan with wolves were 2.3-5.8 deer/km² (Potvin et al., 2005). In Adirondack Park in New York, USA winter deer density estimates ranged were 0- 5.7 deer/km² with most of the park supporting less than 2 deer/km² (Hinton et al., 2022). As our study area was more similar

to Northern Michigan and the Adirondack Park than suburban areas our average deer density estimate of 3.0 deer/km² is comparable. Even on the higher end of our density estimates, including primary period ten (05-07 to 05-20) with 4.8 deer/km², our estimates were similar to those found in other forested areas with hunting, some human development, and natural predators (Figure 5). It is likely that deep winter snows, hunting outside of the protected game preserve, and canid predators are keeping this study population of deer within similar densities to comparable study systems. However, possibly due to the refuge provided by the protected game preserve, our density estimates are at the higher end of the published range for comparable landscapes.

Our data revealed strong temporal dynamics in deer density driven by the seasonal migration of individuals to winter range. Prior to this study, the extent of winter migration by deer in this area was unknown. Although violating model assumptions of closure, the model did capture the exodus of deer in February and their return in mid-March through changes in abundance and density (Figure 5). Northern white-tailed deer often migrate to avoid extreme cold and/or deep snow (Nelson, 1998). These wintering areas often support large numbers of deer in a concentrated area. Studies have recorded deer densities at over-winter sites from 36 deer/km² in southeastern Minnesota to 12 deer/km² in New Brunswick (Augustine and Frelich, 1998; Morrison et al., 2002). In north-central and northeastern United States, deer densities in wintering areas are typically >10 deer/km² (Russell et al., 2001). In our study, although we did not sample the area most deer migrated, it is likely the density was comparable to other studies. However, this migration and the resulting closure violation is important

when interpreting our results. Beginning in late March (03-26), the abundance stabilized at an average of 345 deer (95% CI= 216, 480; SD= 69; CV= 20%) until the end of the study. To quantify the potential seasonal bias in deer abundance estimates, deer should continue to be monitored for at least a year to capture abundance during the summer and autumn seasons. In addition, expanding the study area to include surrounding deer wintering areas would address the population closure concerns related to migration.

For estimating animal densities, coupling the use of camera-traps with SMR modelling is a recent development (Bengsen et al., 2022; Margenau et al., 2022; Whittington et al., 2018). My thesis provides an important test of a method that shows promise for application across multiple systems. In such an assessment, it is essential to evaluate the precision, typically through calculating the coefficient of variation (CV), of results as accuracy cannot be directly measured. Wildlife managers typically strive for a CV threshold of $\leq 20\%$ to improve management decisions based on the abundance estimate (Butler et al., 2020). Our overall CV (i.e., across all primary periods) was 55%, which is 2.75x greater than the accepted minimum CV threshold. This CV was similar to precision estimates of Margenau et al. (2022) who developed this model across three study sites over a three-year study (North Addition Lands: $29\% < CV < 32\%$; Bear Island: $43\% < CV < 53\%$; Florida Panther National Wildlife Refuge: $61\% < CV < 89\%$; based on the reported 95% CI intervals). However, in our study, there was a wide variation amongst individual primary periods, with four periods meeting the threshold criteria of $\leq 20\%$. This variation was due to changes in available data between primary periods. The

primary period with the largest CV (03-12 to 03-25, CV= 49%; Figure 6) only had 12 marked deer with 346 telemetry points to build the stage one model, and only 64 camera detections of deer for the stage two model. This result was due to the movement of deer out of the study site; such violation of the closure assumption likely renders this estimate invalid. In contrast, the primary period with the smallest CV (05-07 to 05-20, CV= 18%; Figure 6) included 26 marked deer with 3566 telemetry points for stage one, and 139 camera detections for the stage two model. To obtain precise estimates it is likely the model needs a minimum of 12 marked deer with 1550 telemetry locations for the first stage of the model and a minimum of 123 independent detections for the second stage of the model based on the four primary periods that had a CV of \leq 20%. That we obtained a CV of \leq 20% for some periods indicates that if the goal is to estimate population abundance for a short-term study when deer movement and behavior is stable, this model offers a reliable option. However, for a long-term monitoring study, caution needs to be applied as temporal variation in deer movement and behavior can greatly influence the precision of the model. These issues could be resolved by using a broader study extent, but with increased cost and logistical constraints.

Factors Influencing Spatial Variation in Deer Density

Few studies have incorporated spatial covariates into their SCR models to estimate the effects of environmental factors on white-tailed deer density (Engebretsen et al., 2023; Johnson et al., 2021). Most studies that have used SCR models and incorporated spatial covariates studied the ecology, density, and distribution of

carnivore species (Proffitt et al., 2015; Royle et al., 2011; Sollmann et al., 2011; Tourani 2022). In addition, many of the SCR models that have linked habitat-density effects used genetic capture-recapture sampling methods, not camera-traps (Kendall et al., 2016; Linden et al., 2018; Brazeal et al., 2017). Our study aimed to address the knowledge gap of linking white-tailed deer density and spatial covariates using SCR methods, specifically using camera-traps, to understand the underlying landscape factors affecting deer density. Further, we aimed to extend the two-stage SMR approach of Margenau et al. (2022) by incorporating spatial covariates.

Deer density appeared to be moderately influenced by broad harvest management strategy when comparing an area protected from licensed hunting and an area that can be hunted. Deer use predator-avoidance strategies in response to hunting pressure during the hunting season (Cromsigt et al., 2013), including moving to refuges where hunting is restricted (Zagata and Haugen, 1974; Root et al., 1988; Rhoads et al., 2013). We expected deer density in our study area to be greater in the game preserve where hunting was restricted. Although the 95% confidence intervals for the effect of the game preserve on density overlapped zero, they did so only slightly, and the effect of the game preserve was in the expected, positive direction (Table 3). Shortly after the conclusion of the hunting season to the end of our study, study cells in the game preserve on average had a 9% higher deer density than those outside. Similarly, others have determined that roughly twice as many female deer restricted their movements to within refuge limits after the hunt compared to 25-30% using the refuge pre-hunt (Rhoades et al., 2013). Their findings indicate deer will selectively move to refuges

during a hunting season and remain in the refuge after the season ends. Our sampled period occurred after the conclusion of the 2021 hunting season (17 days), so hunting pressure should have subsided. Presumably hunting would have a decaying effect on deer behavior after cessation of the hunting season. The deer in our study area could have returned to normal behavior and space use thus reducing the need for seeking refuge in the game preserve. It is also possible that the deer within the game preserve were not deploying predator avoidance strategies, but instead were potential residents within the game preserve. Deer that reside within refuges have higher survival rates than deer that disperse and reside in unprotected areas (Nixon et. al, 1991). In addition, environmental factors could be influencing the effect of the game preserve (e.g. preferred habitat). Further monitoring that overlaps the hunting season could help resolve the influence of the game preserve on deer density and better understand whether deer are selectively moving to the game preserve to avoid hunting pressures, have a higher survival rate inside the game preserve, or the area includes preferred habitat.

Deer often selectively use areas with dense conifer landcover in winter (DelGiudice et al., 2013; Hurst and Porter, 2008; Morrison et al., 2002). In our study area, we expected the same. Indeed, in our model the coniferous land cover covariate was the reference category and we found that deer occurred at lower densities on average in mixed and deciduous forests (Table 3). Water and grassland landcover types had no effect on average density in the study area, suggesting that deer density was positively associated with coniferous forests. Coniferous trees provide better thermal

cover with less snow accumulation (DelGiudice et al., 2013). Deer will use areas abundant with balsam fir, cedar, and hemlock trees. These areas often have better forage availability, albeit less nutritious, during winter compared to mixed forest and deciduous forest areas (Dumont et al., 2005). As such, traditional wintering areas of deer that experience high densities are typically dominated by coniferous trees (Morrison et al., 2002). These coniferous stands are important resources for deer survival in the winter.

For managers, deer-vehicle collisions are a serious concern. Such collisions are a major human safety risk and are an increasing threat in areas with high deer densities and increasing human development (DeNicola and Williams, 2008). We expected that deer would avoid roads and multi-use trails due to the higher mortality risk and increased human presence, but we also expected potential nuances in this relationship since deer will use roads and trails for movement corridors (Hinton et al., 2022).

Although many studies have investigated deer mortality in relation to roads (Feldhamer et al., 1986; Grovenburg et al., 2008; Kautz et al., 2022; McShea et al., 2008; Ng et al., 2008) fewer studies have looked at the direct effect of road or trail density on deer density or distribution. Amongst those studies, there are mixed findings on the effect of road and trail density indicating a context-dependent response to roads and trails.

Several studies have found white-tailed deer abundance increases with road density (Bowman et al., 2010; Fuller et al., 2022; Hinton et al., 2022; Munro et al., 2012). In eastern Ontario, paved road density had a positive influence on relative deer abundance (Munro et al., 2012). Studies in the Boreal Forest have found a positive relationship

between deer abundance and road density, theorizing human-made linear features allow for deer expansion into previously uninhabited areas (Bowman et al., 2010; Fuller et al., 2022). Within Adirondack Park (approximately 24,280 km²) in New York, USA, deer density increased with proximity to roads particularly during winter, with researchers hypothesizing that deer used the roads as travel networks to avoid deeper snow (Hinton et al., 2022). Conversely, our study, working at finer scales (approximately 16 km²), found that, on average, deer density decreased with increasing road and trail density. In addition, sampling directly on human used trails and roads may lead to bias as animals could be using the linear features for short periods of time to travel between areas, but spend a majority of their time away from these features (Kolowski and Forrester, 2017). When comparing deer mark-recapture abundance estimates between road surveys and camera-traps, road survey abundance estimates were significantly lower than the camera-trap estimates (Roberts et al., 2006). This suggests the deer population was more abundant across the study area than the sampled area near roads.

The drivers of the responses of deer to roads are multi-faceted. As prey species, deer balance tradeoffs between predation risk and forage availability. Roads can decrease natural predator risk as predators often avoid roads (Fahrig and Rytwinski, 2009), but increase the risks of vehicle mortality risk (Kautz et al., 2022) and hunting mortality, given that hunters tend to focus their activities near roads and trails (Lebel et al., 2012; Paton et al., 2017). On the other hand, roads can also increase forage opportunities for deer by increasing edge habitat in forested areas with more productive non-forested vegetation, typically introduced grasses, found in roadside ditches

(Anderson et al., 2013; Ng et al., 2008). However, the predator-prey and forage trade-off is highly dependent on the system and the human use of the area. The deer in our study area likely avoided roads and trails due to the high-use from humans (personal observation), and the likely higher harvest risk along roads in the hunted area. Several of the trails in our study area are popular snow-mobile routes and deer avoid highly trafficked snow-mobile trails (Dorrance et al., 1975). In addition, our study area was well populated by humans, with deer likely avoiding roads due to high vehicular use.

Conclusion

Estimating the abundance of white-tailed deer is challenging for resource management agencies, particularly in heavily forested regions. Instead, agencies often rely on proxies of abundance such as hunter harvest data to monitor population trends and to guide management decisions (Kahlert et al., 2015; Priadka et al., 2020; Stephens et al., 2014). For example, in Ontario hunters are required to report how many days they hunted, how many deer they saw, and whether they were successful (OMNRF, 2017). Managers use this yearly data to decide whether changes in hunter reports warrant changes in management strategy. However, more detailed estimates of deer numbers are necessary to appropriately respond to the increasing threat of climate change and chronic wasting disease (CWD) on deer populations. In the face of these stressors, and specifically CWD, wildlife managers will need to reliably, accurately, and quickly estimate deer population density and abundance. Deer density in particular is essential for understanding the spread and prevalence of infectious diseases (Storm et al., 2013). Conducting seasonal or fine temporal scale estimates will be necessary as deer

movements and distribution can vary dramatically throughout the year. Despite imprecision associated with the model due to migration, our study demonstrates that camera-traps coupled with SCR modelling provide a useful means for managers to estimate deer abundance with the opportunity to link landcover features to better understand environmental effects on population densities. Through repeated sampling, increasing the study area, and longer monitoring, future research can improve precision and document additional temporal changes in covariate effects. We believe that our study points to a valuable opportunity for managers to better understand and respond to the population ecology of white-tailed deer.

Chapter 3: Conclusion

With advancements in technology and statistical modeling, biologists now have a wide range of tools for estimating the abundance of wildlife, along with an improved understanding of their behavior and distribution (Margenau et al. 2022; Royle et al., 2018; Whittington et al., 2018). However, new methods require continued assessment and refinement to ensure their applicability to new contexts. In this thesis, I aimed to address whether camera-traps in conjunction with a recently developed spatial-mark resight (SMR) model were a useful option for estimating white-tailed deer density and abundance in Ontario. In addition, I tested whether spatial covariates could be incorporated into the model to better understand some of the environmental drivers influencing deer density.

Using a combination of radio-telemetry and camera-trap data, I fit a SMR model to estimate the density and abundance of a small population of partially marked white-

tailed deer in central Ontario. During the 140-day study, density and abundance varied by an order of magnitude due to the seasonal movement of deer to and from wintering areas. Due to this movement, the variance of the average abundance estimate (CV= 0.55) was greater than the widely accepted level of a coefficient of variation of ≤ 0.2 . Nevertheless, outside this period of substantial movement, precision was generally acceptable.

Moreover, using a modified version of the SMR model, I determined the effect of environmental factors on deer density. As predicted, deer density was greater in patches of coniferous forest, highlighting the importance of conifers as thermal cover during winter months. Deer density was lower where road and trail density was higher, likely due to the perceived risk of predation. Although marginal, deer density was slightly (9%) higher in the protected game preserve. This could be the result of deer seeking refuge from hunters in the protected game preserve, or higher survival of deer inside the game preserve. Overall, this thesis demonstrates that the SMR model can be applied to deer populations in northern environments, though seasonal movements present some challenges. Further, by including spatial covariates we identified some key factors affecting local deer population density.

A major impetus of this research was to assess the practicality of using camera traps to estimate density in the forested environments that present significant challenges to typical population estimation techniques. The Ontario Ministry of Natural Resources and Forestry does not regularly estimate the abundance or density of deer in the province (OMNRF, 2017). Instead, managers rely on hunter harvest data to monitor

population trends and make management decisions. As such, there is no standardized alternative method for estimating population abundance and density of deer in Ontario. However, with increasing concern for the effect of chronic wasting disease (CWD) on deer populations, wildlife managers will need to reliably estimate local deer density and abundance to make informed decisions (OMNRF, 2019). To control the potential spread and prevalence of the disease in Ontario, and to avoid its endemicity, the province will need to act quickly to contain the disease (Rivera et al., 2019). To do so, Ontario managers must be able to efficiently estimate the density of deer within a containment zone, as the density of individuals is intrinsically linked to the spread of CWD (Storm et al., 2013). Estimating how density varies across the landscape will be key to understanding the potential for spread and allow managers to more effectively deploy population control measures. In addition, continued monitoring of changes in density will allow managers to evaluate the effectiveness of their population control efforts and adjust as needed.

This thesis provides the framework for Ontario wildlife managers to estimate cervid density within a designated CWD containment zone using camera-traps. However, the utility of this method is context dependent. In the event of a positive CWD case, managers will want to estimate population abundance as quickly as possible to develop a targeted management plan (OMNRF, 2019). Although the SMR method can provide precise estimates, the time it takes to produce the final estimate (i.e., 10 week minimum in this case) may be too long. Between camera deployments, radio-collar deployments, data collection, photo review, telemetry review, and model fitting, local managers might

prefer to use a more established method like aerial or road surveys, which will take less time (Forsyth et al., 2022). In addition, Ontario managers would be employing population reduction tactics congruently during the assessment window (OMNRF, 2019). Such a decline in abundance would violate the assumption of closure. However, depending on the season and location of the CWD case detection, the SMR camera-trap method would be advantageous; aerial and road surveys are most practical during the winter with no canopy cover or in non-forested areas. Further, under a scenario where there was a positive case of CWD, it is valid to assume that significant resources could be put towards a more rapid estimation, which would at least expedite steps such as camera deployment and photo ID. Compared to aerial surveys, camera-traps are more cost effective (especially after the initial investment of purchasing cameras), less stressful for wildlife, and safer for personnel (Taylor et al., 2021). In addition, the SMR method provides managers the opportunity to monitor a population over a longer period (Margenau et al., 2022). Most other abundance estimation techniques provide an estimate at a moment in time and do not capture the seasonal or annual fluctuations in abundance. Conversely managers using camera-traps would be able to continue to monitor a population within a containment zone and could determine the success of a population reduction effort with before and after estimates. Further, they could develop a better understanding of the spatial distribution and temporal behaviors of the population. In addition, clinical signs of CWD can take up to two years to present, so if managers continue using camera-traps they could use photos or videos to monitor the population for symptoms (e.g. malnourishment, drooping head, abnormal behavior;

Rivera et al., 2019). Camera-traps are also an advantageous data collection method since they collect data on multiple species at once. This would allow managers to better study areas where there are multiple at-risk cervid species (e.g., moose, elk, deer) (Bengsen et al., 2022).

There may be additional considerations regarding use of the SMR model employed here. We captured, marked, and used radio-collars to track a sub-sample of the population. I used the telemetry locations and resighting history of these individuals in the first stage of the model to estimate priors for the second stage. Not all populations of deer will have the required marked individuals to develop the first stage priors. However, the parameter estimates of λ_0 , the probability of capturing an individual at their activity center, and σ , the rate at which capture probability declines with distance (measured in meters), are key components of the model (Whittington et al., 2018). Managers would either need to capture and mark a sub-sample from the population, use prior estimates from other populations, or approximate λ_0 and σ estimates. Although, in the second stage the marked individual data is not used, treating all deer as unmarked, there could be a loss of precision in the abundance and density estimates if not using λ_0 and σ priors derived from the study population during the same time period (Margenau et al., 2022). In addition, I combined male and female data to estimate an overall population abundance as male and female deer had similar home range sizes during winter and early spring. However, during the rest of the year, males and females employ different space-use and movement strategies. Males tend to increase their home ranges, especially during the rut, to prioritize forage quantity when

access to high-quality forage is risky (Beier and McCullough, 1990; Ofstad et al., 2016). By contrast, females usually have smaller home ranges to care for young, prioritizing high-quality forage and cover (Beier and McCullough, 1990; DePerno et al., 2003). These differences are also highly context dependent (Massé and Côté, 2009). Therefore, as more datum becomes available and the sexes are easier to distinguish (i.e., males with antlers) in photos, the model should be run separately for males and females to better understand the behavioral differences between the sexes.

To address closure assumptions, managers would need to have a general idea of the boundaries of the population they are monitoring, especially if there is seasonal movement to wintering areas. However, unlike other species, deer are not territorial, except for short periods including postpartum for females (Schwede et al., 1993) and during the rut for males (Peterson et al., 2017), so home ranges and extents of the area used by populations are not fixed. Yearling male deer will frequently disperse to new areas, compounding issues of study closure (Oyer et al., 2007). It would be necessary for managers to sample across the entire area in which deer primarily congregate. However, even when increasing a camera grid to cover a larger area to ensure most of the space used by the population is sampled, a population will never truly be closed for long-term monitoring. This is especially true when the sampling period overlaps a period of increased mortality (e.g. hunting season, herd culling) or during the birthing season. Instead, there is also an opportunity to convert the model to an open population model (Efford and Schofield, 2020), which would account for emigration, immigration, births,

and deaths in the population. However, such models are more complex and computationally demanding (Margenau et al., 2022).

This thesis demonstrates the complexity of estimating wildlife abundance and density. It provides an example of how to estimate deer density with camera-traps while incorporating landscape features, but the benefits and drawbacks highlighted above should be considered when using this approach for management decisions. This method provides an additional tool for wildlife managers who are confronting unprecedented levels of environmental threats to the wildlife populations they manage. Advances in research and monitoring allow for more informed decisions, but these advances require continual assessment and refinement to better understand the species and ecosystem dynamics. Conserving wildlife will become more difficult with climate change, environmental degradation, habitat fragmentation, and emerging infectious diseases; we will be better prepared to meet these challenges with the information and knowledge derived from sustained scientific research.

References

- Ågren, E. O., Sörén, K., Gavier-Widén, D., Benestad, S. L., Tran, L., Wall, K., ... & Nöremark, M. (2021). First detection of chronic wasting disease in moose (*Alces alces*) in Sweden. *Journal of Wildlife Diseases*, *57*(2), 461-463.
- Anderson, C. W., Nielsen, C. K., Hester, C. M., Hubbard, R. D., Stroud, J. K., & Schaubert, E. M. (2013). Comparison of indirect and direct methods of distance sampling for estimating density of white-tailed deer. *Wildlife Society Bulletin*, *37*(1), 146-154.
- Augustine, D. J., & Frelich, L. E. (1998). Effects of white-tailed deer on populations of an Avgan, B., Zimmermann, F., Güntert, M., Arikan, F., & Breitenmoser, U. (2014). The first density estimation of an isolated Eurasian lynx population in southwest Asia. *Wildlife Biology*, *20*(4), 217–221.
- Baeten, L. A., Powers, B. E., Jewell, J. E., Spraker, T. R., & Miller, M. W. (2007). A natural case of chronic wasting disease in a free-ranging moose (*Alces alces shirasi*). *Journal of Wildlife Diseases*, *43*(2), 309-314.
- Beaver, J. T., Harper, C. A., Muller, L. I., Basinger, P. S., Goode, M. J., & Van Manen, F. T. (2016). Current and spatially explicit capture-recapture analysis methods for infrared triggered camera density estimation of white-tailed deer. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *3*, 195-202.
- Beier, P., & McCullough, D. R. (1990). Factors influencing white-tailed deer activity patterns and habitat use. *Wildlife Monographs*, 3-51.
- Benestad, S. L., Mitchell, G., Simmons, M., Ytrehus, B., & Vikøren, T. (2016). First case of chronic wasting disease in Europe in a Norwegian free-ranging reindeer. *Veterinary research*, *47*(1), 1-7.
- Bengsen, A. J., Forsyth, D. M., Ramsey, D. S., Amos, M., Brennan, M., Pople, A. R., ... & Crittle, T. (2022). Estimating deer density and abundance using spatial mark–resight models with camera trap data. *Journal of Mammalogy*, *103*(3), 711-722.
- understory forb in fragmented deciduous forests. *Conservation Biology*, *12*(5), 995-1004.
- Bissonette, J. A. (Ed.). (2012). *Wildlife and landscape ecology: effects of pattern and scale*. Springer Science & Business Media.
- Bolger, D. T., Morrison, T. A., Vance, B., Lee, D., & Farid, H. (2012). A computer-assisted system for photographic mark–recapture analysis. *Methods in Ecology and Evolution*, *3*(5), 813-822.
- Borchers, D. L., & Efford, M. (2008). Spatially explicit maximum likelihood methods for capture–recapture studies. *Biometrics*, *64*(2), 377-385.
- Bowman, J., Ray, J. C., Magoun, A. J., Johnson, D. S., & Dawson, F. N. (2010). Roads, logging, and the large-mammal community of an eastern Canadian boreal forest. *Canadian Journal of Zoology*, *88*(5), 454-467.
- Brazeal, J. L., Weist, T., & Sacks, B. N. (2017). Noninvasive genetic spatial capture-recapture for estimating deer population abundance. *The Journal of Wildlife Management*, *81*(4), 629-640.
- Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of computational and graphical statistics*, *7*(4), 434-455.

- Brown, J. S. (1999). Vigilance, patch use and habitat selection: foraging under predation risk. *Evolutionary ecology research*, 1(1), 49-71.
- Burgar, J. M., Stewart, F. E., Volpe, J. P., Fisher, J. T., & Burton, A. C. (2018). Estimating density for species conservation: Comparing camera trap spatial count models to genetic spatial capture-recapture models. *Global Ecology and Conservation*, 15, e00411.
- Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., ... & Boutin, S. (2015). Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52(3), 675-685.
- Butler, M. J., Harris, G. M., Stewart, D. R., Rominger, E. M., & Ruhl, C. Q. (2020). Estimating Sample Size for Point-Count Based Distance Sampling.
- Caravaggi, A., Banks, P. B., Burton, A. C., Finlay, C. M., Haswell, P. M., Hayward, M. W., ... & Wood, M. D. (2017). A review of camera trapping for conservation behaviour research. *Remote Sensing in Ecology and Conservation*, 3(3), 109-122.
- Caravaggi, A., Burton, A. C., Clark, D. A., Fisher, J. T., Grass, A., Green, S., ... & Rivet, D. (2020). A review of factors to consider when using camera traps to study animal behavior to inform wildlife ecology and conservation. *Conservation Science and Practice*, 2(8), e239.
- Cardoso, B., García-Bocanegra, I., Acevedo, P., Cáceres, G., Alves, P. C., & Gortázar, C. (2022). Stepping up from wildlife disease surveillance to integrated wildlife monitoring in Europe. *Research in Veterinary Science*, 144, 149-156.
- Centers for Disease Control and Prevention [CDC]. (2021, October, 18). Prevention | Chronic Wasting Disease. *Center for Disease Control and Prevention*. Retrieved August 12th 2023 from <https://www.cdc.gov/prions/cwd/prevention.html>
- Chandler, R. B., & Royle, J. A. (2013). Spatially explicit models for inference about density in unmarked or partially marked populations. *The Annals of Applied Statistics*, 936-954.
- Clover, M. R. (1956). Single-gate deer trap. *Calif. Fish and Game J.*, 42, 199-201.
- Coffey, M. A., & Johnston, G. H. (1997). A planning process for managing white-tailed deer in protected areas: integrated pest management. *Wildlife Society Bulletin*, 433-439.
- Corcoran, E., Winsen, M., Sudholz, A., & Hamilton, G. (2021). Automated detection of wildlife using drones: Synthesis, opportunities and constraints. *Methods in Ecology and Evolution*, 12(6), 1103-1114.
- Connelly, J.W., Gammonley, J.H., & Keegan, T.W. (2012). Harvest Management. In N.J, Silvy (Ed.). *The Wildlife Techniques Manual* (7th ed, vol 2, pp. 202- 231). The Johns Hopkins University Press.
- Cromsigt, J. P., Kuijper, D. P., Adam, M., Beschta, R. L., Churski, M., Eycott, A., ... & West, K. (2013). Hunting for fear: innovating management of human-wildlife conflicts. *Journal of Applied Ecology*, 50(3), 544-549.
- Cullingham, C. I., Merrill, E. H., Pybus, M. J., Bollinger, T. K., Wilson, G. A., & Coltman, D. W. (2011). Broad and fine-scale genetic analysis of white-tailed deer populations: estimating the relative risk of chronic wasting disease spread. *Evolutionary Applications*, 4(1), 116-131.

- Darlington, S., Ladle, A., Burton, A. C., Volpe, J. P., & Fisher, J. T. (2022). Cumulative effects of human footprint, natural features and predation risk best predict seasonal resource selection by white-tailed deer. *Scientific Reports*, *12*(1), 1072.
- Dawe, K. L., Bayne, E. M., & Boutin, S. (2014). Influence of climate and human land use on the distribution of white-tailed deer (*Odocoileus virginianus*) in the western boreal forest. *Canadian Journal of Zoology*, *92*(4), 353-363.
- Dawe, K. L., & Boutin, S. (2016). Climate change is the primary driver of white-tailed deer (*Odocoileus virginianus*) range expansion at the northern extent of its range; land use is secondary. *Ecology and evolution*, *6*(18), 6435-6451.
- DelGiudice, G. D., Fieberg, J. R., & Sampson, B. A. (2013). A long-term assessment of the variability in winter use of dense conifer cover by female white-tailed deer. *PLoS One*, *8*(6), e65368.
- DeNicola, A. J., & Williams, S. C. (2008). Sharpshooting suburban white-tailed deer reduces deer–vehicle collisions. *Human-Wildlife Conflicts*, *2*(1), 28-33.
- DePerno, C. S., Jenks, J. A., & Griffin, S. L. (2003). Multidimensional cover characteristics: is variation in habitat selection related to white-tailed deer sexual segregation? *Journal of Mammalogy*, *84*(4), 1316-1329.
- de Valpine, P., D. Turek, C.J. Paciorek, C. Anderson-Bergman, D. Temple Lang, and R. Bodik. (2017). Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics* *26*: 403-413. <DOI:10.1080/10618600.2016.1172487>.
- DeVivo, M. T., Edmunds, D. R., Kauffman, M. J., Schumaker, B. A., Binfet, J., Kreeger, T. J., ... & Cornish, T. E. (2017). Endemic chronic wasting disease causes mule deer population decline in Wyoming. *PLoS One*, *12*(10), e0186512.
- Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., ... & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27-46.
- Dumont, A., Ouellet, J. P., Crête, M., & Huot, J. (2005). Winter foraging strategy of white-tailed deer at the northern limit of its range. *Ecoscience*, *12*(4), 476-484.
- Dupke, C., Bonenfant, C., Reineking, B., Hable, R., Zeppenfeld, T., Ewald, M., & Heurich, M. (2017). Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. *Ecography*, *40*(8), 1014-1027.
- Edmunds, D. R., Kauffman, M. J., Schumaker, B. A., Lindzey, F. G., Cook, W. E., Kreeger, T. J., ... & Cornish, T. E. (2016). Chronic wasting disease drives population decline of white-tailed deer. *PloS one*, *11*(8), e0161127.
- Efford, M. (2004). Density estimation in live-trapping studies. *Oikos*, *106*(3), 598-610.
- Efford, M. G., & Schofield, M. R. (2020). A spatial open-population capture-recapture model. *Biometrics*, *76*(2), 392-402.
- Engebretsen, K. N., Cherry, M. J., Conner, L. M., Garrison, E. P., Miller, K. V., & Chandler, R. B. (2023). Noninvasive camera data and spatial capture–recapture models reveal strong temporal variation in fawn survival. *Ecosphere*, *14*(4), e4497.
- Environment and Climate Change Canada. (2022). Daily Data Report 2022 Peterborough Trent U. Retrieved July 7, 2023, from https://climate-weather-gc-ca.proxy1.lib.trentu.ca/climate_data/daily_data_e.html?hlyRange=2005-05-

[12%7C2023-07-06&dlyRange=2005-05-17%7C2023-07-05&mlyRange=2006-04-01%7C2006-12-01&StationID=43763&Prov=ON&urlExtension= e.html&searchType=stnName&optLimit=yearRange&StartYear=2022&EndYear=2023&selRowPerPage=25&Line=0&searchMethod=contains&txtStationName=PETERBOROUGH+TRENT+U&timeframe=2&Day=1&Year=2022&Month=1#](#)

- Fahrig, L., & Rytwinski, T. (2009). Effects of roads on animal abundance: an empirical review and synthesis. *Ecology and society*, 14(1).
- Flagel, D. G., Belovsky, G. E., & Beyer, D. E. (2016). Natural and experimental tests of trophic cascades: gray wolves and white-tailed deer in a Great Lakes forest. *Oecologia*, 180, 1183-1194.
- Feldhamer, G. A., Gates, J. E., Harman, D. M., Loranger, A. J., & Dixon, K. R. (1986). Effects of interstate highway fencing on white-tailed deer activity. *The Journal of Wildlife Management*, 497-503.
- Forsyth, D. M., Comte, S., Davis, N. E., Bengsen, A. J., Côté, S. D., Hewitt, D. G., ... & Mysterud, A. (2022). Methodology matters when estimating deer abundance: a global systematic review and recommendations for improvements. *The Journal of Wildlife Management*, 86(4), e22207.
- Fuller, H. W., Frey, S., & Fisher, J. T. (2023). Integration of aerial surveys and resource selection analysis indicates human land use supports boreal deer expansion. *Ecological Applications*, 33(1), e2722.
- Garrott, R. A., White, P. J., & White, C. A. V. (1993). Overabundance: an issue for conservation biologists?. *Conservation biology*, 946-949.
- Goode, M. J., Beaver, J. T., Muller, L. I., Clark, J. D., Van Manen, F. T., Harper, C. A., & Basinger, P. S. (2014). Capture-recapture of white-tailed deer using DNA from fecal pellet groups. *Wildlife Biology*, 20(5), 270–278. <https://doi.org/10.2981/wlb.00050>
- Glover-Kapfer, P., Soto-Navarro, C. A., & Wearn, O. R. (2019). Camera-trapping version 3.0: current constraints and future priorities for development. *Remote Sensing in Ecology and Conservation*, 5(3), 209-223.
- Green, A. M., Chynoweth, M. W., & Şekercioğlu, Ç. H. (2020). Spatially explicit capture-recapture through camera trapping: a review of benchmark analyses for wildlife density estimation. *Frontiers in Ecology and Evolution*, 8, 563477.
- Grovenburg, T. W., Jenks, J. A., Klaver, R. W., Monteith, K. L., Galster, D. H., Schauer, R. J., ... & Delger, J. A. (2008). Factors affecting road mortality of white-tailed deer in eastern South Dakota. *Human-Wildlife Conflicts*, 2(1), 48-59.
- Haley, N. J., & Hoover, E. A. (2015). Chronic wasting disease of cervids: current knowledge and future perspectives. *Annu. Rev. Anim. Biosci.*, 3(1), 305-325.
- Herrando-Pérez, S., Delean, S., Brook, B. W., & Bradshaw, C. J. A. (2012). Density dependence: an ecological Tower of Babel. *Oecologia*, 170(3), 585–603.
- Hinton, J. W., Hurst, J. E., Kramer, D. W., Stickles, J. H., & Frair, J. L. (2022). A model-based estimate of winter distribution and abundance of white-tailed deer in the Adirondack Park. *Plos One*, 17(8), e0273707.
- Hobbs, R. J., Hallett, L. M., Ehrlich, P. R., & Mooney, H. A. (2011). Intervention ecology: applying ecological science in the twenty-first century. *BioScience*, 61(6), 442-450.

- Hofmann, G. S., Coelho, I. P., Bastazini, V. A. G., Cordeiro, J. L. P., & de Oliveira, L. F. B. (2016). Implications of climatic seasonality on activity patterns and resource use by sympatric peccaries in northern Pantanal. *International Journal of Biometeorology*, *60*, 421-433.
- Horsley, S. B., Stout, S. L., & DeCalesta, D. S. (2003). White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications*, *13*(1), 98-118.
- Howe, E. J., Buckland, S. T., Després-Einspenner, M. L., & Kühn, H. S. (2017). Distance sampling with camera traps. *Methods in Ecology and Evolution*, *8*(11), 1558-1565.
- Hurst, J. E., & Porter, W. F. (2008). Evaluation of shifts in white-tailed deer winter yards in the Adirondack region of New York. *The Journal of Wildlife Management*, *72*(2), 367-375.
- Janousek, W. M., Graves, T. A., Berman, E. E., Chong, G. W., Cole, E. K., Dewey, S. R., ... & Cross, P. C. (2021). Human activities and weather drive contact rates of wintering elk. *Journal of Applied Ecology*, *58*(3), 667-676.
- Johnson, J. T., Chandler, R. B., Conner, L. M., Cherry, M. J., Killmaster, C. H., Johannsen, K. L., & Miller, K. V. (2021). Effects of bait on male white-tailed deer resource selection. *Animals*, *11*(8), 2334.
- Joly, D. O., Ribic, C. A., Langenberg, J. A., Beheler, K., Batha, C. A., Dhuey, B. J., ... & Samuel, M. D. (2003). Chronic wasting disease in free-ranging Wisconsin white-tailed deer. *Emerging Infectious Diseases*, *9*(5), 599.
- Kahlert, J., Fox, A. D., Heldbjerg, H., Asferg, T., & Sunde, P. (2015). Functional responses of human hunters to their prey—why harvest statistics may not always reflect changes in prey population abundance. *Wildlife biology*, *21*(6), 294-302.
- Karanth, K. U. (1995). Estimating tiger *Panthera tigris* populations from camera-trap data using capture—recapture models. *Biological conservation*, *71*(3), 333-338.
- Karanth, K. U., Nichols, J. D., Kumar, N. S., & Hines, J. E. (2006). Assessing tiger population dynamics using photographic capture—recapture sampling. *Ecology*, *87*(11), 2925-2937.
- Kautz, T. M., Fowler, N. L., Petroelje, T. R., Beyer, D. E., Duquette, J. F., & Belant, J. L. (2022). White-tailed deer exploit temporal refuge from multi-predator and human risks on roads. *Ecology and Evolution*, *12*(7), e9125.
- Kendall, K. C., Macleod, A. C., Boyd, K. L., Boulanger, J., Royle, J. A., Kasworm, W. F., ... & Graves, T. A. (2016). Density, distribution, and genetic structure of grizzly bears in the Cabinet-Yaak Ecosystem. *The Journal of Wildlife Management*, *80*(2), 314-331.
- Kolowski, J. M., & Forrester, T. D. (2017). Camera trap placement and the potential for bias due to trails and other features. *PLoS one*, *12*(10), e0186679.
- Kowalewski, L. K., Chizinski, C. J., Powell, L. A., Pope, K. L., & Pegg, M. A. (2015). Accuracy or precision: implications of sample design and methodology on abundance estimation. *Ecological modelling*, *316*, 185-190.
- Lebel, F., Dussault, C., Massé, A., & Côté, S. D. (2012). Influence of habitat features and hunter behavior on white-tailed deer harvest. *The Journal of wildlife management*, *76*(7), 1431-1440.

- Lincoln, F. C. (1930). *Calculating waterfowl abundance on the basis of banding returns* (No. 118). US Department of Agriculture.
- Linden, D. W., Sirén, A. P., & Pekins, P. J. (2018). Integrating telemetry data into spatial capture–recapture modifies inferences on multi-scale resource selection. *Ecosphere*, *9*(4), e02203.
- Little, A. R., Webb, S. L., Demarais, S., Gee, K. L., Riffell, S. K., & Gaskamp, J. A. (2016). Hunting intensity alters movement behaviour of white-tailed deer. *Basic and Applied Ecology*, *17*(4), 360-369.
- Locke, S.L., Parker, I.D. & Lopez, R.R. (2012). Use of Remote Cameras in Wildlife Ecology. In N.J, Silvy (Ed.). *The Wildlife Techniques Manual* (7th ed, vol 2, pp. 311- 318). The Johns Hopkins University Press.
- Lovely, K. R., Mcshea, W. J., Lafon, N. W., & Carr, D. E. (2013). Land parcelization and deer population densities in a rural county of Virginia. *Wildlife Society Bulletin*, *37*(2), 360-367.
- Margenau, L. L., Cherry, M. J., Miller, K. V., Garrison, E. P., & Chandler, R. B. (2022). Monitoring partially marked populations using camera and telemetry data. *Ecological Applications*, *32*(4), e2553.
- Massé, A., & Côté, S. D. (2009). Habitat selection of a large herbivore at high density and without predation: trade-off between forage and cover?. *Journal of Mammalogy*, *90*(4), 961-970.
- Mawdsley, J. R. (2020). Phylogenetic patterns suggest broad susceptibility to chronic wasting disease across Cervidae. *Wildlife Society Bulletin*, *44*(1), 152-155.
- McDonald, L.L., Erickson, W.P., Boyce, M.S. & Alldredge, R.J. (2012). Modeling Vertebrate Use of Terrestrial Resources. In N.J, Silvy (Ed.). *The Wildlife Techniques Manual* (7th ed, vol 2, pp. 310- 428). The Johns Hopkins University Press.
- McShea, W. J. (2012). Ecology and management of white-tailed deer in a changing world. *Annals of the New York Academy of Sciences*, *1249*(1), 45-56.
- McShea, W. J., Stewart, C. M., Kearns, L. J., Licciol, S., & Kocka, D. (2008). Factors affecting autumn deer–vehicle collisions in a rural Virginia county. *Human-Wildlife Conflicts*, *2*(1), 110-121.
- Miller, M. W., & Williams, E. S. (2003). Horizontal prion transmission in mule deer. *Nature*, *425*(6953), 35-36.
- Moeller, A. K., Lukacs, P. M., & Horne, J. S. (2018). Three novel methods to estimate abundance of unmarked animals using remote cameras. *Ecosphere*, *9*(8), e02331.
- Morrison, S. F., Forbes, G. J., & Young, S. J. (2002). Browse occurrence, biomass, and use by white-tailed deer in a northern New Brunswick deer yard. *Canadian Journal of Forest Research*, *32*(9), 1518-1524.
- Morrison, S. F., Forbes, G. J., Young, S. J., & Lusk, S. (2003). Within-yard habitat use by white-tailed deer at varying winter severity. *Forest Ecology and Management*, *172*(2-3), 173-182.
- Murray, M. H., Becker, D. J., Hall, R. J., & Hernandez, S. M. (2016). Wildlife health and supplemental feeding: a review and management recommendations. *Biological Conservation*, *204*, 163-174.

- Nakashima, Y., Fukasawa, K., & Samejima, H. (2018). Estimating animal density without individual recognition using information derivable exclusively from camera traps. *Journal of Applied Ecology*, 55(2), 735-744.
- National Wildlife Health Center. (2023). Expanding Distribution of Chronic Wasting Disease. *USGS science for a changing world*. Retrieved May 26th, 2023 from <https://www.usgs.gov/media/images/distribution-chronic-wasting-disease-north-america-0>
- Nelson, M. E. (1998). Development of migratory behavior in northern white-tailed deer. *Canadian Journal of Zoology*, 76(3), 426-432. Nelson, M. E. (1998). Development of migratory behavior in northern white-tailed deer. *Canadian Journal of Zoology*, 76(3), 426-432.
- Ng, J. W., Nielsen, C., & St. Clair, C. C. (2008). Landscape and traffic factors influencing deer-vehicle collisions in an urban environment. *Human-Wildlife Conflicts*, 2(1), 34-47.
- Nixon, C. M., Hansen, L. P., Brewer, P. A., & Chelsvig, J. E. (1991). Ecology of white-tailed deer in an intensively farmed region of Illinois. *Wildlife monographs*, 3-77.
- O'Connell, A.F., Nichols, J. D., & Karanth, K. U. (2011). *Camera traps in animal ecology: methods and analyses* (Vol. 271). New York: Springer.
- Ofstad, E. G., Herfindal, I., Solberg, E. J., & Sæther, B. E. (2016). Home ranges, habitat and body mass: simple correlates of home range size in ungulates. *Proceedings of the Royal Society B: Biological Sciences*, 283(1845), 20161234.
- Oliver, R. Y., Iannarilli, F., Ahumada, J., Fegraus, E., Flores, N., Kays, R., ... & Jetz, W. (2023). Camera trapping expands the view into global biodiversity and its change. *Philosophical Transactions of the Royal Society B*, 378(1881), 20220232.
- Olson, L. O., Van Deelen, T. R., Storm, D. J., & Crimmins, S. M. (2021). Understanding environmental patterns of canid predation on white-tailed deer (*Odocoileus virginianus*). *Canadian Journal of Zoology*, 99(10), 912-920.
- Ontario Ministry of Natural Resources [OMNR]. (1977). *Petroglyphs Provincial Park Management Plan*.
- Ontario Ministry of Natural Resources and Forestry [OMNRF]. (2017). White-tailed Deer Management Policy for Ontario. *Ontario Government*. Retrieved June 30th, 2023, from chrome-extension://efaidnbmnnnibpcajpcglclefindmkaj/https://files.ontario.ca/mnrf-white-tailed-deer-en-30-01-2020.pdf
- Ontario Ministry of Natural Resources and Forestry [OMNRF]. (2019). Chronic Wasting Disease and Response Plan. *Ontario Government*. Retrieved May 27th, 2023, from <https://files.ontario.ca/mnrf-cwd-prevention-and-response-plan-en-2019.pdf>.
- Ontario Ministry of Natural Resources and Forestry [b. OMNRF]. (2019). White-tailed Deer Population Objective Setting and Harvest Management Guidelines. *Ontario Government*. Retrieved December 18th, 2023, <https://files.ontario.ca/mnrf-white-tailed-deer-population-objective-setting-and-harvest-management-guidelines-en-2020-05-07.pdf>
- Ontario Ministry of Natural Resources and Forestry [a.OMNRF]. (2020). *Forest Management Plan Planning Manual*. Queen's Printer for Ontario.

- Ontario Ministry of Natural Resources and Forestry [b.OMNRF]. (2020). Forest Resources Inventory Packaged Products – Version 2. Bancroft-Minden Forest. [Map]. Retrieved July 7, 2023, from <https://geohub.lio.gov.on.ca/maps/lio::forest-resources-inventory-packaged-products-version-2/about>
- Ontario Ministry of Natural Resources and Forestry [OMNRF]. (2021). *2021 Hunting Regulations Summary Fall 2021 – Spring 2022*.
- Ontario Ministry of Natural Resources and Forestry [OMNRF]. (2022). Ontario Trail Network. Retrieved July 7, 2023 from <https://data.ontario.ca/dataset/ontario-trail-network>
- Ontario Ministry of Transportation [OMT]. (2018). *Wildlife Collision Prevention*.
- Ontario Ministry of Transportation [OMT]. (2020). *Ontario Road Safety Annual Report 2020*.
- Otis, D. L., Burnham, K. P., White, G. C., & Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife monographs*, (62), 3-135
- Oyer, A. M., Mathews, N. E., & Skudt, L. H. (2007). Long-distance movement of a white-tailed deer away from a chronic wasting disease area. *The Journal of wildlife management*, 71(5), 1635-1638.
- Palencia, P., Rowcliffe, J. M., Vicente, J., & Acevedo, P. (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology*, 58(8), 1583-1592.
- Parsons, A. W., Forrester, T., McShea, W. J., Baker-Whetton, M. C., Millspaugh, J. J., & Kays, R. (2017). Do occupancy or detection rates from camera traps reflect deer density?. *Journal of Mammalogy*, 98(6), 1547-1557.
- Paton, D. G., Ciuti, S., Quinn, M., & Boyce, M. S. (2017). Hunting exacerbates the response to human disturbance in large herbivores while migrating through a road network. *Ecosphere*, 8(6), e01841.
- Peel, M. C., Finlayson, B. L., & McMahon, T. A. (2007). Updated world map of the Köppen-Geiger climate classification. *Hydrology and earth system sciences*, 11(5), 1633-1644
- Peterson, B. E., Storm, D. J., Norton, A. S., & Van Deelen, T. R. (2017). Landscape influence on dispersal of yearling male white-tailed deer. *The Journal of Wildlife Management*, 81(8), 1449-1456.
- Pierce, B.L., Lopez, R.R. & Silvy, N.J. (2012). Estimating Animal Abundance. In N.J, Silvy (Ed.). *The Wildlife Techniques Manual* (7th ed, vol 2, pp. 311- 318). The Johns Hopkins University Press.
- Pollock, K. H. (1991). Review papers: modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. *Journal of the American Statistical Association*, 86(413), 225-238.
- Priadka, P., Brown, G. S., Patterson, B. R., & Mallory, F. F. (2020). Sex and age-specific differences in the performance of harvest indices as proxies of population abundance under selective harvesting. *Wildlife Biology*, 2020(3), 1-11.
- Priesmeyer, W. J., Fulbright, T. E., Grahmann, E. D., Hewitt, D. G., DeYoung, C. A., & Draeger, D. A. (2012). Does supplemental feeding of deer degrade vegetation? A

- literature review. In *Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies* (Vol. 66, pp. 107-113).
- Proffitt, K. M., Goldberg, J. F., Hebblewhite, M., Russell, R., Jimenez, B. S., Robinson, H. S., ... & Schwartz, M. K. (2015). Integrating resource selection into spatial capture-recapture models for large carnivores. *Ecosphere*, *6*(11), 1-15.
- R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Reconyx
- Reilly, M. L., Tobler, M. W., Sonderegger, D. L., & Beier, P. (2017). Spatial and temporal response of wildlife to recreational activities in the San Francisco Bay ecoregion. *Biological Conservation*, *207*, 117–126.
- Rhoads, C. L., Bowman, J. L., & Eyler, B. (2013). Movements of female exurban white-tailed deer in response to controlled hunts. *Wildlife Society Bulletin*, *37*(3), 631-638.
- Rieucou, G., Vickery, W. L., Doucet, G. J., & Laquerre, B. (2007). An innovative use of white-tailed deer (*Odocoileus virginianus*) foraging behaviour in impact studies. *Canadian Journal of Zoology*, *85*(7), 839-846.
- Rivera, N. A., Brandt, A. L., Novakofski, J. E., & Mateus-Pinilla, N. E. (2019). Chronic wasting disease in cervids: Prevalence, impact and management strategies. *Veterinary Medicine: Research and Reports*, 123-139.
- Roberts, C. W., Pierce, B. L., Braden, A. W., Lopez, R. R., Silvy, N. J., Frank, P. A., & Ransom Jr, D. (2006). Comparison of camera and road survey estimates for white-tailed deer. *The Journal of Wildlife Management*, *70*(1), 263-267.
- Rooney, T. P. (2009). High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecology*, *202*, 103-111.
- Root, B. G., Fritzell, E. K., & Giessman, N. F. (1988). Effects of intensive hunting on white-tailed deer movement. *Wildlife Society Bulletin (1973-2006)*, *16*(2), 145-151.
- Rowe, J.S. (1972). "Forest regions of Canada." Canadian Forestry Service publication; no. 1300.
- Rowcliffe, J. M., Field, J., Turvey, S. T., & Carbone, C. (2008). Estimating animal density using camera traps without the need for individual recognition. *Journal of Applied Ecology*, 1228-1236.
- Royle, J. A., Fuller, A. K., & Sutherland, C. (2018). Unifying population and landscape ecology with spatial capture–recapture. *Ecography*, *41*(3), 444-456.
- Royle, J. A., Magoun, A. J., Gardner, B., Valkenburg, P., & Lowell, R. E. (2011). Density estimation in a wolverine population using spatial capture–recapture models. *The Journal of wildlife management*, *75*(3), 604-611.
- Royle, J. A., R. B., Chandler, R. Sollmann, & Gardner, B. (2014). Spatial capture–recapture. Academic Press, Waltham, Massachusetts, USA.
- Royle, J. A., & Young, K. V. (2008). A hierarchical model for spatial capture–recapture data. *Ecology*, *89*(8), 2281-2289.

- Russell, F. L., Zippin, D. B., & Fowler, N. L. (2001). Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *The American Midland Naturalist*, *146*(1), 1-26.
- Satter, C. B., Augustine, B. C., Harmsen, B. J., Foster, R. J., & Kelly, M. J. (2019). Sex-specific population dynamics of ocelots in Belize using open population spatial capture–recapture. *Ecosphere*, *10*(7), e02792.
- Schwede, G., Hendrichs, H., & McShea, W. (1993). Social and spatial organization of female white-tailed deer, *Odocoileus virginianus*, during the fawning season. *Animal Behaviour*, *45*(5), 1007-1017.
- Shelton, A. L., Henning, J. A., Schultz, P., & Clay, K. (2014). Effects of abundant white-tailed deer on vegetation, animals, mycorrhizal fungi, and soils. *Forest Ecology and Management*, *320*, 39-49.
- Sikes, R. S., Thompson, T. A., & Bryan, J. A. (2019). American Society of Mammalogists: raising the standards for ethical and appropriate oversight of wildlife research. *Journal of Mammalogy*, *100*(3), 763-773.
- Sollmann, R., Furtado, M. M., Gardner, B., Hofer, H., Jácomo, A. T., Tôrres, N. M., & Silveira, L. (2011). Improving density estimates for elusive carnivores: accounting for sex-specific detection and movements using spatial capture–recapture models for jaguars in central Brazil. *Biological conservation*, *144*(3), 1017-1024.
- Sorensen, A., van Beest, F. M., & Brook, R. K. (2014). Impacts of wildlife baiting and supplemental feeding on infectious disease transmission risk: a synthesis of knowledge. *Preventive veterinary medicine*, *113*(4), 356-363.
- Spraker, T. R., Miller, M. W., Williams, E. S., Getzy, D. M., Adrian, W. J., Schoonveld, G. G., ... & Merz, P. A. (1997). Spongiform encephalopathy in free-ranging mule deer (*Odocoileus hemionus*), white-tailed deer (*Odocoileus virginianus*) and Rocky Mountain elk (*Cervus elaphus nelsoni*) in northcentral Colorado. *Journal of wildlife diseases*, *33*(1), 1-6.
- Stan Development Team (2023). RStan: the R interface to Stan. R package version 2.21.8. <https://mc-stan.org/>.
- Statistics Canada. (2021). National Road Network. Retrieved July 7, 2023 from <https://open.canada.ca/data/en/dataset/3d282116-e556-400c-9306-ca1a3cada77f>
- Statistics Canada.(2022). Census Profile 2021 Census of Population: North Kawartha, Township Ontario. Retrieved August 26, 2023 from <https://www12.statcan.gc.ca/census-recensement/2021/dp-pd/prof/details/page.cfm?Lang=E&GENDERlist=1,2,3&STATISTIClist=1,4&HEADERlist=0&DGUIDlist=2021A00053515037&SearchText=North%20Kawartha>
- Stephens, P. A., Pettorelli, N., Barlow, J., Whittingham, M. J., & Cadotte, M. W. (2015). Management by proxy? The use of indices in applied ecology. *Journal of Applied Ecology*, *52*(1), 1-6.
- Storm, D. J., Samuel, M. D., Rolley, R. E., Shelton, P., Keuler, N. S., Richards, B. J., & Van Deelen, T. R. (2013). Deer density and disease prevalence influence transmission of chronic wasting disease in white-tailed deer. *Ecosphere*, *4*(1), 1-14.

- Taylor, J. C., Bates, S. B., Whiting, J. C., McMillan, B. R., & Larsen, R. T. (2022). Using camera traps to estimate ungulate abundance: a comparison of mark–resight methods. *Remote Sensing in Ecology and Conservation*, 8(1), 32-44.
- The North America Land Change Monitoring System [NALCMS]. 2023. 2020 Land cover of north America at 30 meters. Retrieved July 7, 2023 from <http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2020/>
- Tompkins, D. M., Carver, S., Jones, M. E., Krkošek, M., & Skerratt, L. F. (2015). Emerging infectious diseases of wildlife: a critical perspective. *Trends in parasitology*, 31(4), 149-159.
- Tourani, M. (2022). A review of spatial capture–recapture: Ecological insights, limitations, and prospects. *Ecology and Evolution*, 12(1), e8468.
- Thompson, A. K., Samuel, M. D., & Van Deelen, T. R. (2008). Alternative feeding strategies and potential disease transmission in Wisconsin white-tailed deer. *The Journal of Wildlife Management*, 72(2), 416-421.
- Vercauteren, K. C., Anderson, C. W., Van Deelen, T. R., Drake, D., Walter, W. D., Vantassel, S. M., & Hygnstrom, S. E. (2011). Regulated commercial harvest to manage overabundant white-tailed deer: An idea to consider?. *Wildlife Society Bulletin*, 35(3), 185-194.
- Vélez, J., Castiblanco-Camacho, P. J., Tabak, M. A., Chalmers, C., Fergus, P., & Fieberg, J. (2022). Choosing an Appropriate Platform and Workflow for Processing Camera Trap Data using Artificial Intelligence. *arXiv preprint arXiv:2202.02283*.
- Vikøren, T., Våge, J., Madslie, K. I., Røed, K. H., Rolandsen, C. M., Tran, L., ... & Benestad, S. L. (2019). First detection of chronic wasting disease in a wild red deer (*Cervus elaphus*) in Europe. *Journal of wildlife diseases*, 55(4), 970-972.
- Weiskopf, S. R., Ledee, O. E., & Thompson, L. M. (2019). Climate change effects on deer and moose in the Midwest. *The Journal of Wildlife Management*, 83(4), 769-781.
- Whittington, J., Hebblewhite, M., & Chandler, R. B. (2018). Generalized spatial mark–resight models with an application to grizzly bears. *Journal of Applied Ecology*, 55(1), 157-168.
- Wild, M. A., Hobbs, N. T., Graham, M. S., & Miller, M. W. (2011). The role of predation in disease control: a comparison of selective and nonselective removal on prion disease dynamics in deer. *Journal of Wildlife Diseases*, 47(1), 78-93.
- Wildlife Insights. (2021). About Wildlife Insights AI. *Wildlife Insights*. Retrieved July 7, 2023 from <https://www.wildlifeinsights.org/about-wildlife-insights-ai>
- WildTrax.(2023). About Us. *WildTrax*. Retrieved July 7, 2023 from <https://wildtrax.ca/about/>
- Williams, E. S., & Miller, M. W. (2002). Chronic wasting disease in deer and elk in North America. *Revue scientifique et technique (International Office of Epizootics)*, 21(2), 305-316.
- Williams, E. S., & Young, S. (1980). Chronic wasting disease of captive mule deer: a spongiform encephalopathy. *Journal of Wildlife Diseases*, 16(1), 89-98.
- Williams, S. C., Denicola, A. J., Almendinger, T., & Maddock, J. (2013). Evaluation of organized hunting as a management technique for overabundant white-tailed deer in suburban landscapes. *Wildlife Society Bulletin*, 37(1), 137-145.

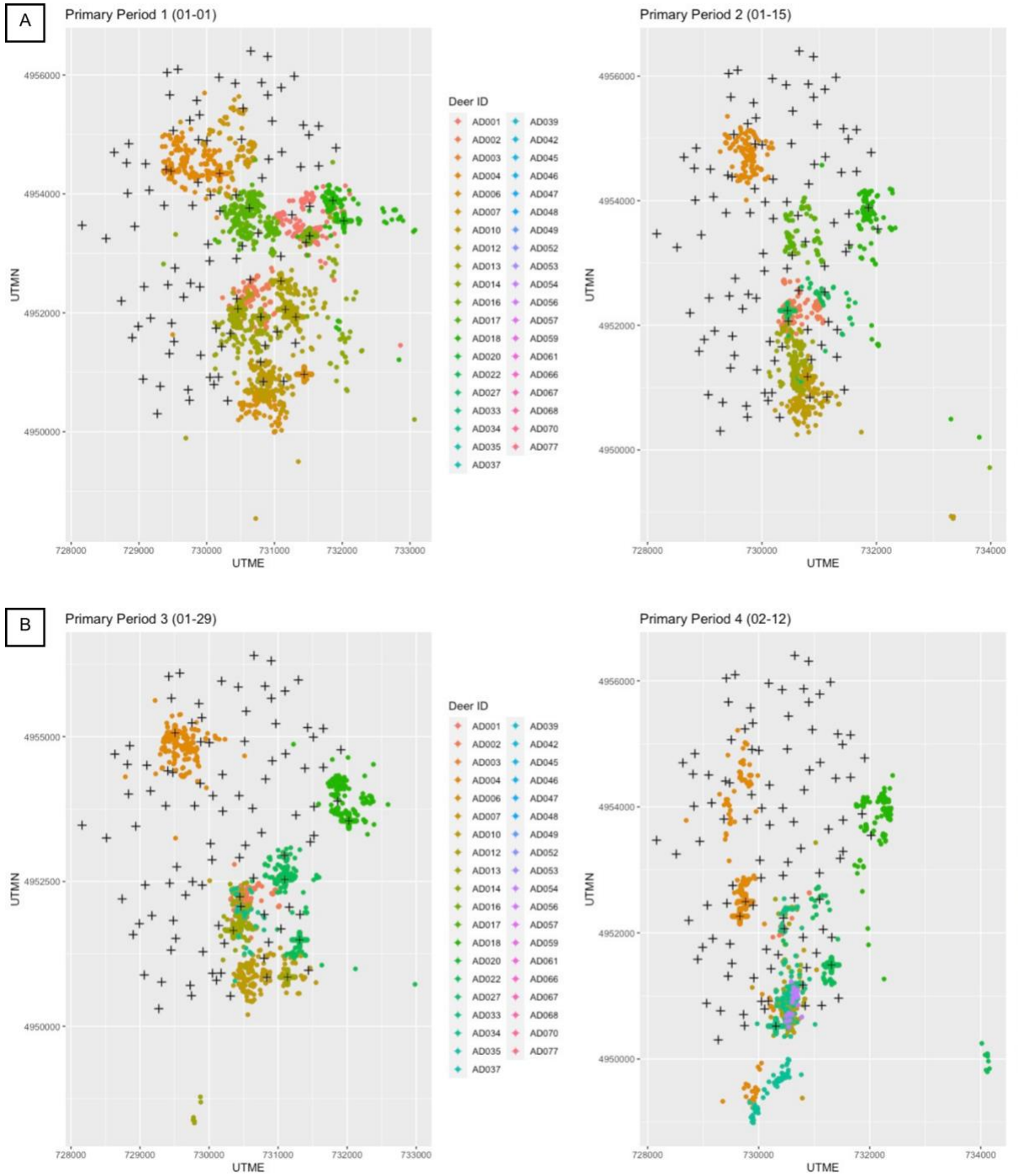
- Wong, B. B. M., & Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, 26(3), 665–673. <https://doi.org/10.1093/beheco/aru183>
- Zagata, M. D. & Haugen, A. O. (1974) White-Tailed Deer Movement at Pilot Knob State Park, Iowa. *Proceedings of the Iowa Academy of Science*, 81(2), 76-82.

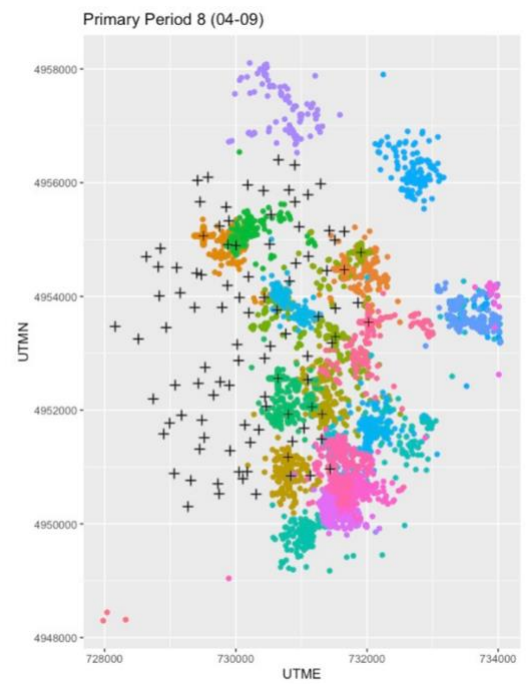
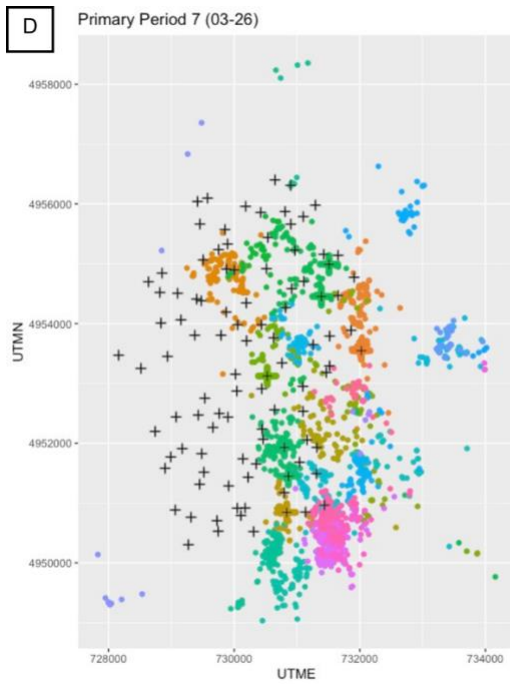
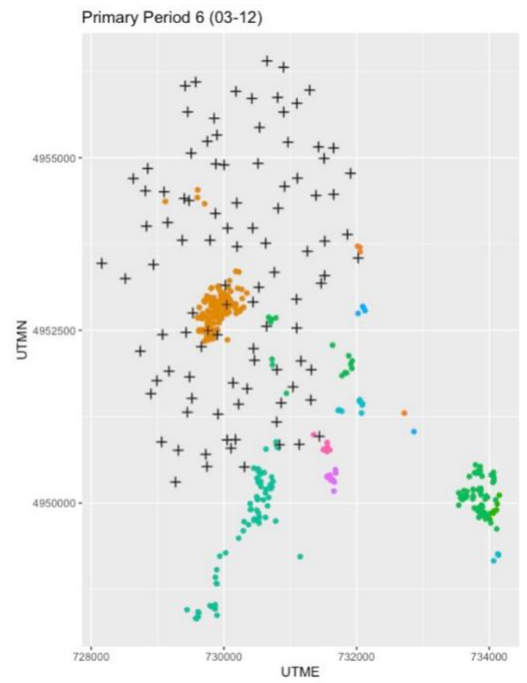
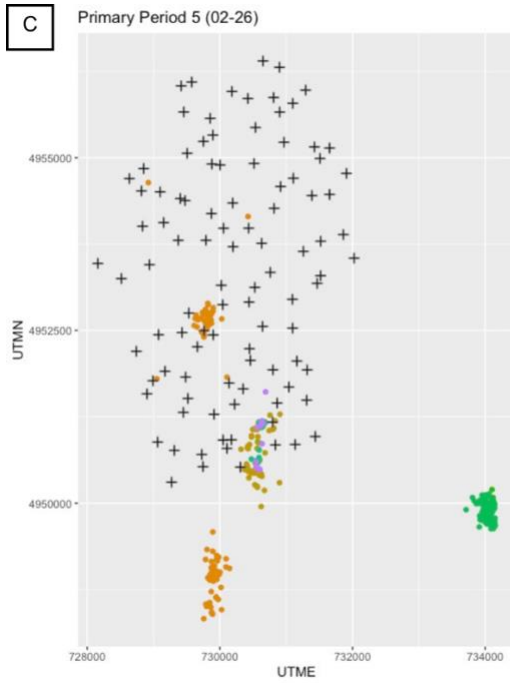
Appendix

Table A1. Results of the MCP test and Wilcoxon signed-rank test comparing average male and female 95% MCP spaced used estimates for each two-week primary period. Bonferroni adjusted alpha for analyzing significance was 0.005 ($\alpha=0.05/10$) Month and day represent the start of the primary period.

		Primary Periods (MM-DD)									
		01-01	01-15	01-29	02-12	02-26	03-12	03-26	04-09	04-23	05-07
Male (km ²)	Mean	12.14	23.41	2.25	3.34	1.67	5.89	22.80	1.72	1.27	2.01
	SD	19.17	36.48	2.79	2.74	1.92	9.46	23.42	1.10	0.39	1.40
Female (km ²)	Mean	5.03	16.94	2.45	1.66	6.81	5.22	31.83	1.51	1.17	1.06
	SD	10.03	29.26	3.14	1.65	14.64	9.62	47.79	1.72	0.74	0.54
P-Value		0.35	0.74	0.99	0.18	0.18	0.66	0.76	0.29	0.25	0.03

Note: P ≤ 0.005 significant value denoted by (*)





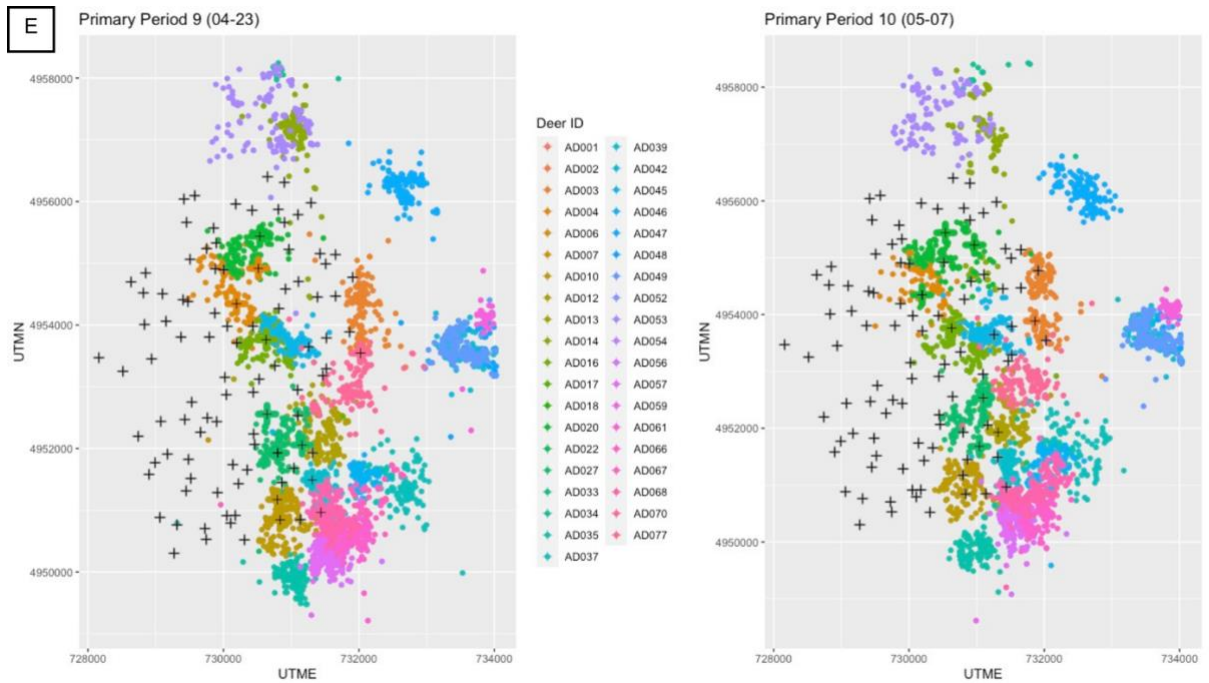


Figure A1. Visual representation of the Stage 1 telemetry points from the 39 radio-collared deer who were within the study area boundary, including the 2-km buffer, at least once during the 140-day study period. Each map represents the GPS points of the collared deer for each two-week primary period (MM-DD; first day of the primary period). The pluses represent the camera-trap locations. If a deer was resighted by a camera-trap during the primary period it is denoted with the corresponding deer id color surrounding the camera-trap location. All camera-trap and GPS points are configured in UTM.

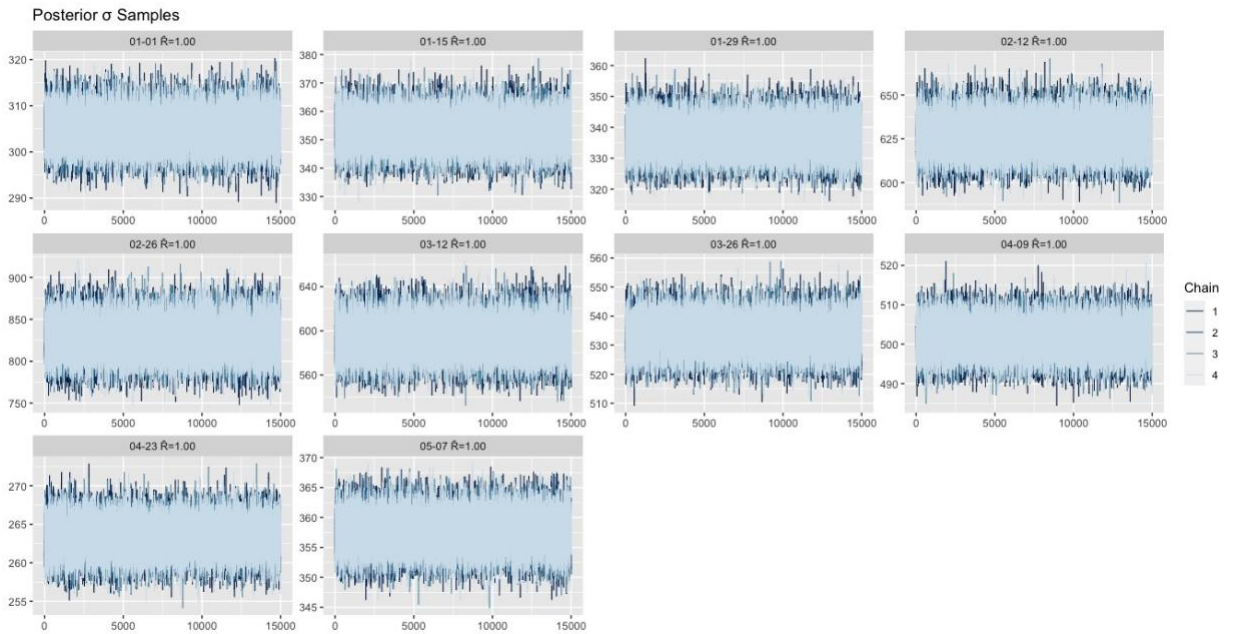


Figure A2. Stage 1 SCR models for all ten two-week primary periods (MM-DD) converged based on posterior σ samples from four chains of 15,000 iterations with corresponding Gelman-Rubin convergence statistic ($\hat{R} < 1.05$). Month and day represent the start of the primary period.

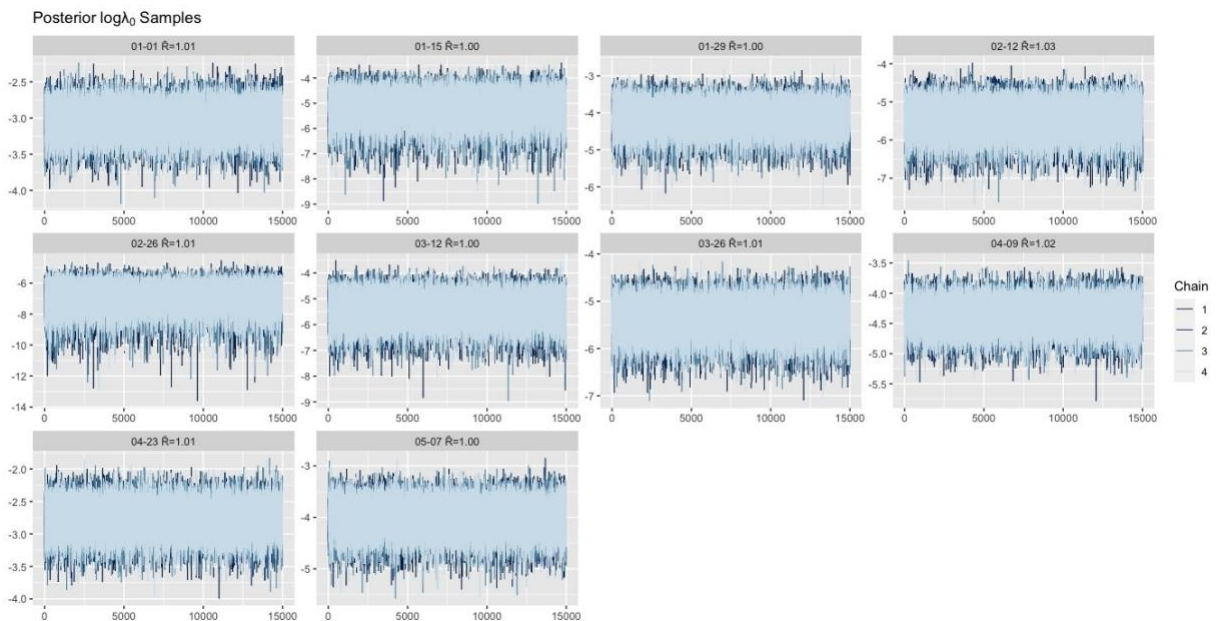


Figure A3. Stage 1 SCR models for all ten two-week primary periods (MM-DD) converged based on posterior $\log \lambda_0$ samples from four chains of 15,000 iterations with corresponding Gelman-Rubin convergence statistic ($\hat{R} < 1.05$). Month and day represent the start of the primary period.

Table A2. Stage 1 parameter summary statistics averaged across the 10 two-week primary periods including the mean, median, standard deviation (SD), 95% confidence intervals (CI) of parameter estimates.

Stage 1 Parameter	Mean	Median	SD	Lower CI	Upper CI
σ	469.74	431.53	169.63	261.80	841.83
$\beta_0 \log \sigma$	5.876	5.938	0.329	5.21	6.41
$\alpha \sigma$	0.587	0.645	0.280	-0.08	0.97
$\varepsilon \sigma$	0.413	0.379	0.130	0.24	0.69
$\log \lambda_0$	-4.644	-4.594	1.264	-7.40	-2.59
$\beta_0 \log \lambda_0$	-4.455	-4.453	0.556	-5.53	-3.22
$\alpha \lambda_0$	0.336	0.350	0.338	-0.42	0.92
$\varepsilon \lambda_0$	1.345	1.303	0.348	0.78	2.08

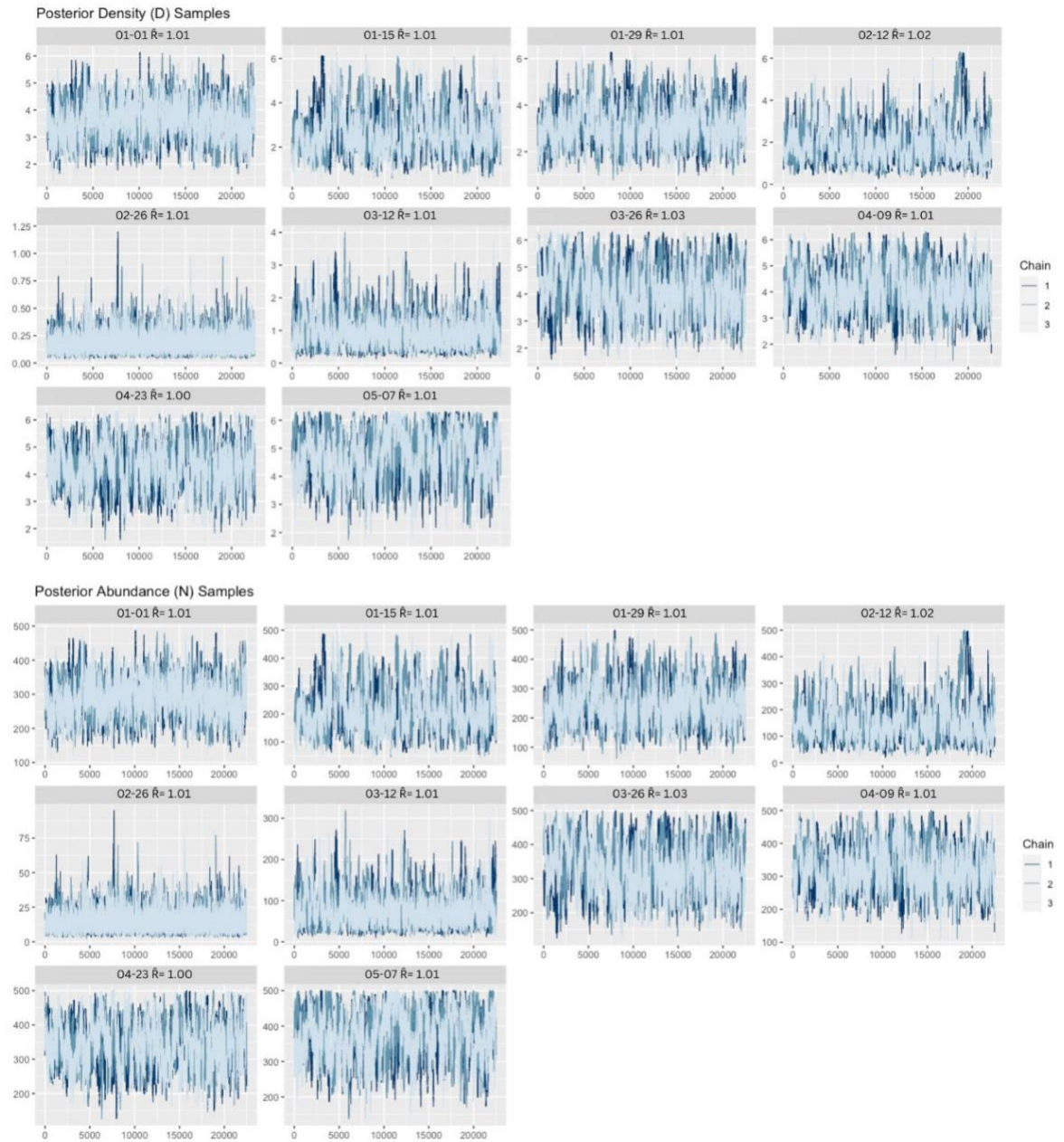


Figure A4. Stage 2 SCR models for all ten two-week primary periods (MM-DD) converged based on posterior density (D) and abundance (N) samples from three chains of 22,500 iterations with corresponding Gelman-Rubin convergence statistic ($\hat{R} < 1.05$).