

Assessing the drivers of white-tailed deer (*Odocoileus virginianus*) migration: Exploring  
changing predation risk and food availability in an Ontario population

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## Abstract

Assessing the drivers of white-tailed deer (*Odocoileus virginianus*) migration: Exploring changing predation risk and food availability

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Animal migration is defined as the seasonal movement from one independent and non-overlapping range to another. Understanding how and why animals migrate is important not only to understand their life history processes but also for informing other important ecological processes such as the spread of wildlife disease and habitat alteration. Animal migrations have been impacted by human activity with instances of complete loss of migrations in human-altered areas. Understanding the drivers of migration can help predict responses to future environmental changes and potentially help conserve these phenomena. Seasonal movements of white-tailed deer (deer; *Odocoileus virginianus*; Zimmerman, 1780) have been linked to seasonal changes in environmental conditions that impact their ability to find food resources and risk of predation. The *human shield* hypothesis posits that prey species will select habitat close to people to use predator fear of humans to protect themselves from predation. Using global positioning system (GPS) collars, we examined the onset of deer migrations and assessed how environmental variables including snow, temperature, and plant biomass influenced migration departure dates using time-to-event models. We compared deer locations to data from GPS collared coyotes (*Canis latrans*; Say, 1823) within the same study area to explore daily space-use differences and examine if deer migrations were food or predation-risk driven using generalized linear mixed effects regression models. We found substantial annual and individual variation in deer migration dates. Snow

depth was the strongest and most consistent predictor of deer migration, with individuals departing earlier with greater snow depth. Our regression analyses showed that deer selected for habitats closer to and with greater density of anthropogenic structures than coyotes at all times. After removing the animal locations close to areas with active supplemental feeding, these effects were diminished showing no differences in proximity or density of structures. Overall, we found more support for a food driven migration rather than a predator driven *human shield*. With the reduction in natural food caused by snow cover, we suggest that supplemental feeding is likely influencing the use of wintering areas by deer. The high proportion of deer migrating to human developed areas with supplemental feeders highlights the need for continued research into the impacts of human activity on animal behaviour.

**Keywords:** white-tailed deer, coyote, human shield, migration, supplemental feeding

## **Land Acknowledgement**

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As a visiting graduate student, I have an important responsibility to acknowledge the grounds on which I have been granted access to use in the pursuit of higher education and research. Trent University and my study area are in the traditional and treaty territory of the Mississauga's (Williams Treaty and Crawford Purchase). I believe that it is important to recognize the Mississauga for their care for and teachings about the flora and fauna within their territory. I will honor that care throughout my fieldwork and when writing about my research. Considering their deep spiritual history and understanding the role of Treaty People, I will dedicate myself to moving forward in the spirit of collaboration, and reconciliation.

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## Acknowledgement

A mere page in the acknowledgement section of this thesis falls short of adequately recognizing everyone who has assisted me over the past 2.5 years. However, as I digress, this thesis is dedicated to my wife Jackie and our “secret” son Theo, who was born in the middle of my first field season. Although you did not choose to complete this masters, thank you for enduring it with me.

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## **Chapter 1: General Introduction (2024)**

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### **Animal Migration**

Understanding the movement of animals and how their environment influences these movements is critical to the study of ecology and evolution. Animals whose life histories include migrations can access resources that would be unavailable otherwise and avoid hazardous conditions, thereby increasing their fitness (Lack, 1968, Fryxell et al. 1988, Rettie and Messier, 2000, Dingle and Drake, 2007, Newton, 2008). The term migration typically calls to mind the long-distance movements by ungulates such as caribou and wildebeest. However, migrations vary across species and depend on individual species ecology and environmental context. Migrants can be obligate or conditional (Dingle and Drake, 2007), thus, the definition of migration should be based on the behaviour and physiology of the animal rather than just their spatial pattern (Dingle, 1996). For the purposes of this thesis, I define migration as the temporary relocation of an animal between two non-overlapping home ranges (Kauffman et al. 2021).

Many migrating species play important roles in ecosystem processes. For example, the influx of ungulates foraging on their seasonal range can increase light availability and nutrients for plants (McNaughton, 1979). Therefore, impacts to migrations can have consequences at the ecosystem level (Harris et al. 2009). Migrations around the world are at risk because of human impacts on habitat such as the creation of barriers (e.g. dams, fences), overexploitation of migrants, and climate

change (Robinson et al. 2009, Kubelka et al. 2022). However, most migrating species are not at risk of immediate extinction but instead they are becoming less abundant (Wilcove and Wikelski, 2008). Because of their positive contributions to ecosystems, protecting the abundance of migrating species and routes is important in maintaining ecosystem health (Wilcove and Wikelski, 2008).

### **Study Species**

White-tailed deer (*Odocoileus virginianus*, deer, *Zimmermann 1780*) are the most abundant ungulate in Ontario, Canada and in several other North American jurisdictions (VerCauteren, 2003, Hewitt, 2011, OMNRF, 2017). Deer act as a keystone species, influencing the structure and composition of forest communities and in turn, play a fundamental role in trophic dynamics (Rooney and Waller, 2003, Fligel et al. 2016). The Ontario range of deer spans from the southern edge of the heavily forested boreal and into the province's deforested farmlands (Kennedy-Slaney et al. 2018).

Deer are a prey species and their potential predators in Ontario include wolves (*Canis lupus*), coyotes (*Canis latrans*), and black bear (*Ursus americanus*). Predation is the primary source for juvenile mortality of deer throughout North America (Kautz et al. 2019); however, in some areas, humans have disrupted natural predator-prey spatial dynamics, through land-use change, thus creating a *human shield* (Berger, 2007, Muhly et al. 2011, Shannon et al. 2014). When predator behaviours shape the distribution of prey, the relationship is classified as a trait-mediated direct effect (Schmitz et al. 1997, Preisser and Bolnick 2008). Predators and prey have competing behavioural interests, where prey try to minimize and predators try to maximize their overlap (Sih, 2005). Some prey species like moose (*Alces alces*) may select for areas in close proximity to

humans, in landscapes where grizzly bear (*Ursus arctos horribilis*) densities are high (Berger, 2007). These trait-mediated indirect effects of human impacts have the potential to modify the direct interactions between species (Dill et al. 2003, Muhly et al. 2011). Kautz et al. (2019) found that areas with human development reduced predation on white-tailed deer fawns by coyotes.

White-tailed deer also play important cultural and social roles in Ontario and beyond (Hewitt, 2015). During colonization, deer hides became used as a currency for trade between the settling Europeans and existing indigenous communities, and their meat for a food source, which remains highly sought after to this day (Hewitt, 2015). Today, white-tailed deer hold significance in Ontario's economy through recreational hunting, vehicle collisions and, agricultural damage (Palmer et al. 1982, Conover et al. 1995, Grado et al. 2007). Additionally, deer can be important in the spread of disease, often acting as hosts or vectors (Medrano et al. 2012, Kugeler et al. 2016). Therefore, understanding white-tailed deer behaviour is fundamental to managing many economic, cultural, ecological and wildlife disease issues.

One of the primary contemporary issues facing deer in North America is the spread of Chronic wasting disease (CWD). This fatal and transmissible neurodegenerative disease of cervids was first detected in North America in the 1960's and has since spread to at least 26 US states and four Canadian provinces (Miller et al. 2000, Belsare et al. 2021). Cervid populations decline in areas where CWD becomes endemic (Conner and Miller, 2004, Gagnier et al. 2020). Further, the disease can lead to reductions in hunter participation primarily due to the perceived risk of transmission to humans (Vaske et al. 2004, Erickson et al. 2019). A reduction in hunter interest may

lead to social and economic consequences and subsequently reduced conservation and management funding through loss of license revenue (Erickson et al. 2019). To manage the spread of CWD, wildlife managers have attempted numerous tactics including culling infected populations to reduce contact rates and placing restrictions on hunters to limit movement of infected animals (Gagnier et al. 2020).

### **White-tailed deer migration**

White-tailed deer at the northern extent of their range migrate in response to adverse weather and seasonal changes in food availability (Marchinton and Hirth, 1984, Nelson, 1995, Sabine et al. 2002). Not all deer migrate, and individuals are classified as conditional versus obligate migrators (Dingle and Drake, 2007, Fieberg et al. 2008). Migration in deer is thought to be a learned behaviour, with fawns learning the strategy by migrating with their mothers (Nelson, 1994, 1998). Deer are thought to migrate to enable access to seasonally higher quality habitat, possibly leading to greater reproductive success (Nicholson et al. 1997).

Earlier studies suggest that the primary cues for migration to wintering areas by deer are declining temperatures or increasing snow depth (Sabine et al. 2002, Fieberg et al. 2008). Additionally, the onset of spring migration has been linked to snowmelt (Hoskinson and Mech, 1976, Nelson et al. 2004). These variable environmental conditions are thought to be connected to changing food availability, increased energetic requirements in deeper snow, and predator avoidance. In some instances when northern white-tailed deer migrate, they travel to winter yards and congregate, forming communal trails that lessen the impacts of navigating through deep snow (Sabine et al. 2002). Deer will seek areas out that provide thermal cover and access to

nutritious food (Nixon, 2008). Predators of deer often capture more deer during severe winters with deep snow, so yarding has also been considered an anti-predator strategy (Hoskinson and Mech 1976, Fryxell et al. 1988, Sabine et al. 2002, Morrison et al. 2003).

Seasonal change in vegetation is also a potential proximate driver of migration (Hoskinson and Mech, 1976, Nelson, 1995; Nicholson et al. 1997). Specifically, the forage maturation hypothesis states that energy gain is maximized at intermediate levels of biomass where the trade off between forage quantity with forage quality is optimal (Fryxell, 1991). There are seasonal differences in the timing of when vegetation is most nutritious, which makes migrating ungulates stage in areas with delayed phenology to ensure longer access to the most nutritious forage (Hebblewhite et al. 2008). This phenomenon has been reported to occur in many ungulates (Sawyer and Kauffman, 2011, Bischof et al. 2012) and can be measured through changes in the normalized differential vegetation Index (NDVI), or the *greenness* of vegetation.



## Research Design

As human populations increase along with their impacts on deer and their habitats, the causes and consequences of migration are likely impacted. With technological advancements, the proximate causes of ungulate migration can now be studied in high detail. Using GPS telemetry collars, we explored the causes of deer migration, focusing on both the timing and drivers of migration, and further investigated the potential for predator shielding by humans as the ultimate determinant driving deer to migrate. There are two primary mechanisms that we hypothesized could be driving migration and that we wanted to test between. First, we hypothesized that food availability could be driving migration, with deer moving to their winter ranges when food on their summer range became inaccessible and deer moving back to their winter range when the availability of young forage started to increase. If deer use food availability as their primary cue to initiate the onset of migration, then, we expect an increase in migration activity during periods of high snow accumulation, temperature fluctuations and significant changes in spring plant biomass due to their established links with food availability. Second, we hypothesized that predation could be driving migration, whereby deer would migrate to their winter range when snow became deep enough to impede movement and make them more vulnerable and return to their summer range when predation risk was reduced due to the melting snow. If deer use predation risk as their primary migration cue, then, during the winter, we predict deer will migrate to areas closer to and in higher density of structures than coyotes, using the structures as a predator shield.

## **Chapter 2: Exploring white-tailed deer (*Odocoileus virginianus*) migration behaviours in Ontario, Canada (2023)**

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### **Introduction**

Animal migrations, defined here as the temporary movement of an animal between two non-overlapping home ranges (Dingle, 1996, Kauffman et al. 2021), are an adaptive response that allows individuals to exploit shifting resources (Nicholson et al. 1997). Animal migrations are disappearing (Wilcove and Wikelski, 2008; Bolger et al. 2008), with the main threats being human impacts on habitat, the creation of barriers, overhunting and climate change (Robinson et al. 2009, Kubelka et al. 2022). Thus, there is a clear need to better understand how migratory species might adapt to future changes.

Several ungulate species are known to migrate, including white-tailed deer (*Odocoileus virginianus*), moose (*Alces alces*), elk (*Cervus canadensis*) and caribou (*Rangifer tarandus*) (Sweanor and Sandegren, 1988, Fieberg et al. 2008, Rayl et al. 2021, Michelot et al. 2023). In northern climates, seasonally variable environmental conditions such as plant biomass and snow are the proximate drivers of ungulate migrations (Parker et al. 1984, Albon and Langvatn 1992, Hebblewhite et al. 2008). Ultimate causes of migratory behaviour in ungulates include: forage, thermal exposure, and predation (Fryxell et al. 1988, Monteith et al. 2011, Kauffman et al. 2021).

White-tailed deer are one of the most widespread ungulates in North America and exist across a wide range of landscapes (Côté et al. 2004, Habeck and Shultz 2015). At the northern extent of their range, some white-tailed deer populations are migratory, likely due to the strong seasonal contrasts in environmental conditions (Marchinton and Hirth 1984, Nelson 1995, Sabine et al. 2002). There is evidence that deer migrations and yarding behaviour have developed both as an antipredator strategy and as a way for deer to access seasonal forage in response to severe winters (Messier and Barrette, 1985, Fryxell and Sinclair, 1988, Sabine et al. 2002, Jones et al. 2014, Smolko et al. 2018). As with most migratory species, deer initiate seasonal migration in response to environmental cues, such as cold temperatures, and increasing snow depth (Sabine et al. 2002, Fieberg et al. 2008). The seasonal changes in the availability of forage are one of the best studied factors influencing ungulate migration (Hoskinson and Mech, 1976, Nelson 1995; Nicholson et al. 1997). Many studies on ungulates, posit that migration is strongly influenced by the selection for high quality forage. The forage maturation hypothesis (FMH) states that intermediate biomass levels should provide the highest quality forage for deer by striking a balance between forage intake and digestibility (Fryxell, 1991). However, for many ungulates, access to premium quality forage is ephemeral (Fryxell, 1991, Monteith et al. 2018). *Surfing the green wave* describes a migratory strategy whereby animals attempt to follow the maturation plants to optimize energy intake (Van der Graaf et al. 2006, Bischof et al. 2012).

Some white-tailed deer populations migrate from summer ranges to winter yards, congregating together to navigate deep snow with communal trails and seek areas with thermal cover and access to nutritious food (Sabine et al. 2002, Morrison et al. 2003,

Fieberg et al. 2008, Nixon 2008). Although improved access to forage is a clear driver of ungulate migrations, predation risk also plays an important role. Deer that choose poor quality yards have been known to be predisposed to coyote predation (Messier and Barrette, 1985, Lavigne, 1992). The risk of predation has also been found to be positively linked with winter severity (Nelson and Mech, 1981, Messier and Barrette, 1985). Thus, travelling to winter yards can be seen as an anti-predator strategy by deer (Hoskinson and Mech, 1976, Messier and Barrette, 1985, Fryxell et al. 1988, Patterson and Messier 2000, Sabine et al. 2002). During migration, deer also are exposed to a high risk of predation, as they travel between seasonal ranges (Nelson and Mech, 1981). Prey animals like deer must balance access to forage with risk of predation (Olson et al. 2021). In some areas, humans have disrupted natural predator-prey spatial dynamics through landscape development by creating a *human shield* (Berger, 2007). This term describes the creation of areas with lower predation risk when predators alter their space use to avoid humans and their infrastructure (Berger, 2007, Shannon et al. 2014). In one example, deer that selected for fawning areas near human development experienced a reduction in neonatal predation by coyotes (Kautz et al. 2019).

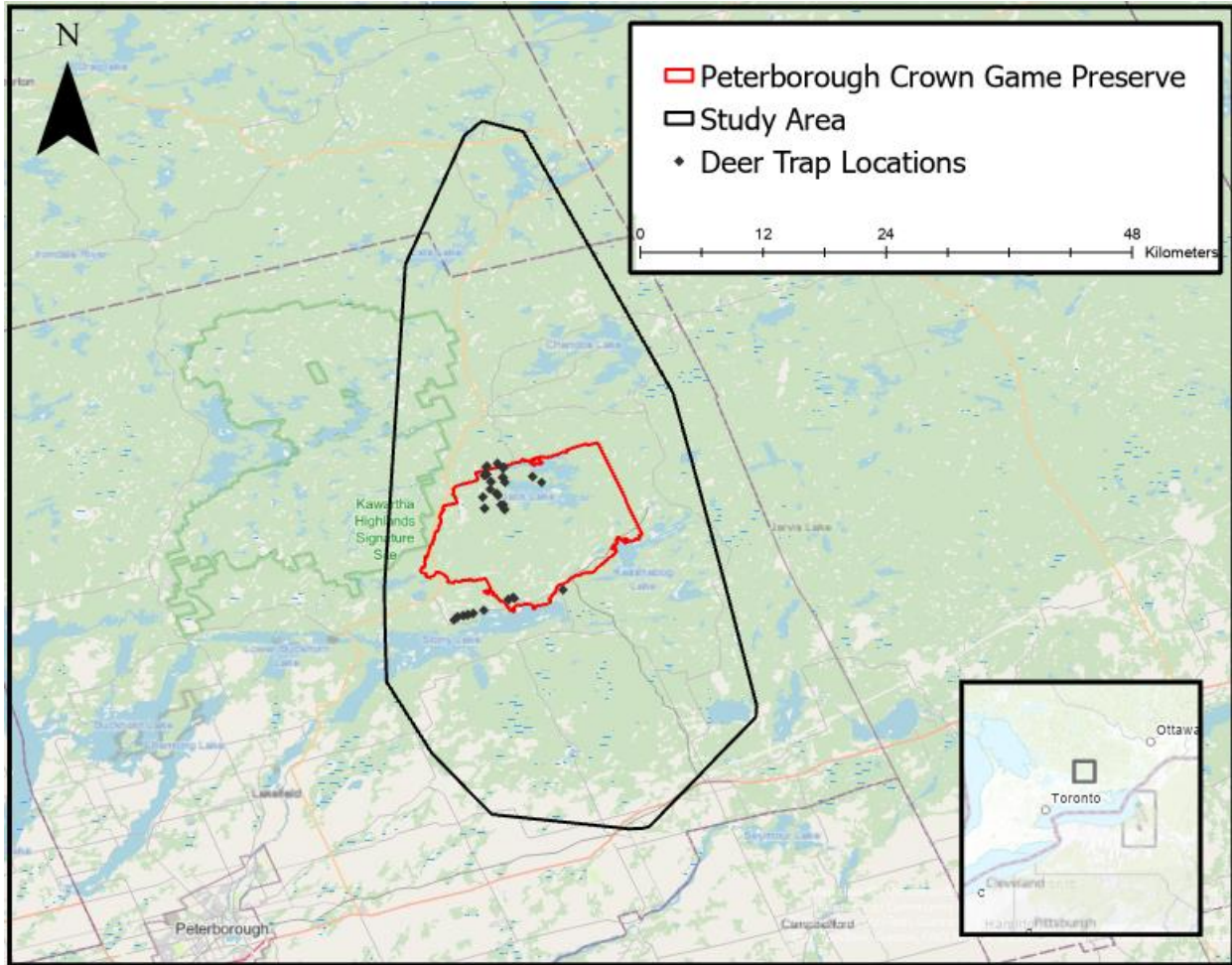
Our primary objective was to improve understanding of the factors driving white-tailed deer migration in central Ontario, Canada. We aimed to quantify the effect of environmental variables on the probability of deer migration and sought to understand whether migration was ultimately related more strongly to predation risk or food availability. To assess predation risk, we examined seasonal changes in spatial overlap of collared deer and coyotes across migratory ranges and quantified the impact of

human activity during winter on the observed space use of GPS-collared deer and coyotes. We also examined if deer migration was influenced by food availability by incorporating identified supplemental feeding areas into our analyses. Given the high rates of coyote predation on white-tailed deer in the area, we predicted that deer in our study would migrate in response to changing conditions that affected their predation risk.

## Methods

### Study Area

Our study was conducted within and immediately surrounding the Peterborough Crown Game Preserve (game preserve) in Ontario, Canada (Figure 1). This area lies within Ontario's wildlife management units (WMU's) 60 and 74B. The game preserve is 152km<sup>2</sup> and composed of 80% public land outside of parks, 10% provincial park land and 10% private land. The game preserve has no hunting outside of a small Indigenous hunt for subsistence, but hunting was allowed throughout the remainder of the study area. There are numerous roads, ATV and snowmobile trails that run throughout the study area and there were active logging operations during the study (2021-2023, OMNRF). The study area is primarily forested (79%), with large areas of open water (12%), with 3% barren land, 3% wetland and 3% urban (2015 Canada Land Cover). The forests are mixed deciduous and coniferous, with the most common tree species being Eastern White Pine (*Pinus strobus*), followed by Red Oak (*Quercus rubra*), Hard Maple (*Acer saccharum*), Eastern White Cedar (*Thuja occidentalis*), Red Pine (*Pinus resinosa*), and Poplar (*Populus sp*) (FRI OMNRF 2019). Predators of deer in the area included eastern coyotes (*Canis latrans*) and American black bear (*Ursus americanus Pallas, 1780*). Other mammals observed by remote camera traps in the study area include moose (*Alces alces*), bobcat (*Lynx rufus*), fisher (*Pekania pennanti*), marten (*Martes martes*), squirrels (*Sciuridae sp.*), and raccoons (*Procyon lotor*) (Bullington 2023).



**Figure 1:** The area used to study white-tailed deer and coyote interactions in south-eastern Ontario, Canada between December 2021, and May 2023. The boundary represents a minimum convex polygon surrounding all deer GPS locations. The locations used to trap deer are also shown.

### Field Methods (White-tailed deer)

White-tailed deer were captured in modified Clover traps (Clover, 1954) deployed within and adjacent to the game preserve (Figure 1). Clover traps were baited according to the *Guidelines for Winter Feeding of Deer in Ontario* document (OMNRF, 1997) to avoid known health complications from winter feeding (Butler et al. 2008). Clover traps

were monitored using cellular-enabled remotely triggered cameras (Spypoint Inc., model link-micro-lte) and staff attended traps upon detection of deer within traps on the camera. All white-tailed deer were physically restrained by two handlers, hobbled using leather belts and blindfolded. Some deer (n=13) were chemically immobilized using aspirated intranasal xylazine at a dose of 1.5ml for adults and 1.0ml for fawns (West et al. 2014) while all remaining animals were physically restrained only for processing. Once restrained, an ear tissue sample was taken using a 5-millimetre biopsy punch. The capture and handling protocol was approved under the Trent University and Ontario Ministry of Natural Resources and Forestry Animal Care Committees, protocol #s 21-460, 22-460, 23-460. All age and sex classes of white-tailed deer were fitted with Lotek Litetrack 420 GPS collars with 8 of these collars having integrated video cameras (Lotek Wireless Inc). During the December 2021 to April 2022 trapping season, doe collars were sized at 37cm +/- 4cm and bucks were sized at 41cm +/- 4cm. During the second field season from December 2022 to April 2023, collar sizes were reduced by 4cm for a tighter fit. All collars were Iridium linked, programmed to log the identify of any other collars within 1m, equipped with a triaxial accelerometer programmed to record raw acceleration data every 15 seconds, and had timed drop-off mechanisms installed, programmed to drop after 2 years. These units also could be remotely triggered to release. All buck collars were fitted with magnetic expanders of variable length (5, 12 or 18cm) depending on collar size, animal size and age. Lastly, collars were spliced and reattached with a piece of ¼ inch rubber tubing acting as a failsafe if the drop-off mechanisms failed. Fawn collars were fitted with foam to further reduce the collars size and allow for additional growth within the 2-year deployment interval. Collars were set



to attempt a GPS fix every 2 hours and were programmed to send mortality alerts if the collar did not move for more than 6 hours. Only GPS points with a dilution of precision value of 8 or less were retained for analyses: this ensured that all points were accurate to between 4 and 14 meters (Jung et al. 2018).

**Field Methods (Coyotes)** - Coyotes were captured and collared using 4-coiled Victor #3 soft-catch foothold traps equipped with a drag chain and hook. Traps were placed along accessible trails, with commercial scents or lures used as bait, and discreetly concealed to maintain a natural appearance. Once captured, a 1:1 mixture of Ketamine (conc = 100 mg/ml; dosage = 5 mg/kg): Medetomidine (conc = 1 mg/ml; dosage = 0.05 mg/kg) was used to chemically immobilize the coyotes. Atipamezole (concentration = 5 mg/ml; dosage = 0.2 mg/kg) was used for reversal. Lotek LiteTrack Iridium 360 (Lotek Wireless Inc.) and Vectronic Survey Globalstar 1C (Vectronic Aerospace) collars were deployed on the coyotes. Coyote collaring was approved by the OMNRF Wildlife Animal Care Committee, protocol #'s (21-75, 22-75, 23-75). Coyote collars attempted a GPS fix every 4 hours. Collars were programmed to send mortality alerts if the collar did not move for more than 6 hours.

### **Relatedness Estimates of Deer**

DNA from collared deer were genotyped at 16 loci (Cullingham et al. 2011) and their relatedness was estimated using the Queller and Goodnight (1989) method. All fawn – adult female pairs for which the coefficient of relatedness was estimated at  $> 0.3$  were treated as mother- offspring pairs. Migrating fawns for which we did not capture their assumed mother were treated as unique migrating deer in our time-to-event model (below). When both members of a doe fawn pair were collared, the collared fawns were

dropped from our regression analyses to avoid pseudoreplication. This follows the assumption that all fawns will migrate following their mothers (Nelson 1994).

**Statistical Analysis** – We took a multi-stage analytical approach to identify the proximate drivers of migration and to assess the potential ultimate causes. Specifically, we were interested in inferring if deer were migrating to reduce predation risk or to access improved food resources. To do this, we first used a time-to-event model (Kasza et al. 2014) which allowed us to assess the relative influence of different environmental covariates on the probability of deer migration. If migrations were food driven, we would expect covariates impacting food availability to have strong statistical relationships with migration probability. Conversely, if the migrations were predator driven, we would expect strong relationships with covariates closely associated with changes in predation risk. We also investigated changes in habitat use across their seasonal ranges: this approach allowed a coarse assessment of changes in factors driving behavior on different seasonal ranges and thus potential insight to drivers of migration. Specifically, we assessed seasonal changes in spatial overlap with radio-collared coyotes, using a mixed effects regression model, to infer if migration was occurring to reduce predation risk. Finally, we re-ran the same models after applying a data filter to exclude areas within a 1km radius of known supplemental feeding sites. This additional step was taken to distinguish between the influences of food availability and predator avoidance on migration patterns because both factors were highly linked to human structures.

**Time-to-Event Analysis** - To model the probability of migration of white-tailed deer, we used time-to-event models fit in a Bayesian framework (adopted from Fieberg and DelGiudice, 2008) using the R statistical software (R Development Core Team 2024).

Deer migrations were defined as seasonal movements, > 2 km, from one independent and non-overlapping range to another, and we modeled both autumn to winter and winter to spring movements (Fieberg, 2008). The autumn to winter (north to south) migration date range was defined as the earliest date when a deer departed for their winter range to when the last deer arrived (December 17<sup>th</sup> to March 2<sup>nd</sup>). The winter-spring migration date range was defined as the earliest date when a deer initiated the return to their summer range to the date when the last deer returned (March 10<sup>th</sup> to April 6<sup>th</sup>). We extended these ranges to include 5 days prior to the date of the earliest migration to ensure the inclusion of conditions when deer were not migrating. We calculated the probability of initiating migration on a given day, or earlier, as the sum of conditional probabilities of migration for each day of the seasonal date interval.

We included the average daily temperature, average daily snow depth, and normalized difference vegetation Index (NDVI), an indirect estimate of gross plant production (Borowik et al. 2013), as potential covariates explaining the probability of a deer migrating on a given day. We obtained data on average daily temperature and daily snow depth from the Environment and Natural Resources portal of the Government of Canada, from the Apsley, Ontario weather station. NDVI values were taken from the USGS EROS Archive - Vegetation Monitoring - eVIIRS Global NDVI (<https://earthexplorer.usgs.gov/>, accessed: July 2023). All model covariates were standardized by subtracting the mean and dividing by the standard deviation. We modelled the daily probability of migration, with days coded as 0 when deer did not migrate and 1 when they migrated. Covariate effects were modeled using a proportional hazards formulation (Cox, 1972, Heisey et al. 2007, Fieberg and DelGiudice, 2008). We

compared models with no covariates to those with all the covariates using the leave one out information criterion (LOOIC), following the approach of Vehtari et al. (2017). We used LOOIC to determine if the inclusion of the covariates chosen improved the model's predictive performance. Additionally, we examined pairwise Pearson's correlations between covariates. If any were correlated at ( $|r| > 0.6$ ) we calculated the condition number of the covariate matrix to determine the degree of collinearity (Salmeron et al. 2018, Visscher et al 2023). If the condition number of the matrix was greater than 5, redundant covariates were removed (Lazaridis 2007).

***Habitat Use by Coyotes and White-tailed deer*** – We modelled the influence of human-built structures on differences in habitat use by deer and coyotes. A structure was defined as any erected building visible by satellite imagery or included in the municipal lot fabric layer. We digitized all structures using a combination of satellite imagery and municipal lot fabric layers (ESRI, 2024, Peterborough County GIS Mapper, 2024) within an area containing all GPS locations of collared deer. We then quantified the number of structures within a 1km buffer around each individual animal location to calculate structure density and the average daily distance to structures (average distance between all locations in a day and the closest structure). We identified locations where supplemental feeding was occurring in the wintering part of our study area via an aerial survey. All linear features in the study area were flown in a Eurocopter EC130 helicopter and the location of supplemental feeding sites were record using a GPS. While searching for track aggregations, the helicopter maintained a speed between 90-110knots and an altitude of 300 feet above ground. Once tracks were spotted, the EC130 helicopter slowed to <20knots and dropped altitude to 150-200 feet,

to record the feeding locations. In addition to the pilot, the aerial survey was conducted with a navigator sitting in the front and two back observers (left and right), looking for feeding locations.

We used a Wilcoxon rank-sum test to test for differences in the density and distance to structures between coyotes and deer. We used an alpha value of 0.05 to determine significance. To further assess these differences while accounting for other potentially important covariates and multiple measures per individual, we fit separate hierarchical regression models to the distance and density data for each species. We included covariates for day vs night (*day\_night*), winter vs summer ranges (*season*) and deer vs coyote (*species*). For the *species* covariate: *coyotes* were coded as 0, and *deer* were coded as 1. For the *season* covariate: *summer range* was coded as 0, and *winter range* was coded as 1. For the *day\_night* covariate: *daytime* was coded as 0, and *nighttime* was coded as 1. Daytime was defined as between 0600 and 1900 for the summer and 0700 – 1800 for the winter. Season was defined as summer (April 12 to December 15) and winter (January 15 to March 30). We included interactions between all covariates including a 3-way interaction among *day\_night*, *season*, and *species*.

When measuring the factors that influenced distances to structures, we used a linear mixed-effect regression model (LMER) with a random intercept for each individual and random slopes for all main effects and interactions except for the main effect of *species*. To quantify the factors influencing the density of structures, we used a generalized linear mixed effect regression model (GLMER) with a Poisson distribution and the same random intercepts and slopes as for the linear model. Both models were fit using the *lme4* package in R (Bates et al. 2015). We removed all GPS locations of

both white-tailed deer and coyotes within a 1km buffer around each identified supplemental feeding location and then re-ran the LMER and GLMER models. We did this to assess whether habitat use patterns were robust regardless of the presence of supplemental feed in close proximity.

## Results

Between December 2021 and April 2023, we captured and collared 156 deer including 61 adult females, 24 adult males, 12 yearling females, 4 yearling males, 38 female fawns, and 29 male fawns. From these captured deer, we were able to follow 20 unique adult males and 65 adult female white-tailed deer during their spring (2022 and 2023) and autumn (2021 and 2022) migrations. We observed 54 individuals in the autumn migration period (going from northern summer range to southern wintering range) of December 15 - March 2, of which 44 made migrations. In the spring migration period (deer leaving their winter range in the south to move back north to their summer range) of March 10 to April 6, we followed 75 individuals of which 64 made migrations. The distance of migrations ranged from 3.7km to 41.4km, with an average distance of 14.2 km. For the 2021/2022 winter, the date interval was December 19<sup>th</sup> to March 2<sup>nd</sup> (Autumn to Winter) and March 10<sup>th</sup> to April 6<sup>th</sup> (Winter to Summer).

We then used locations from 148 collared white-tailed deer and 13 collared coyotes within our study area between December 15, 2021, and April 17, 2023, to model the differences in habitat use by each species throughout the year. We excluded five resident deer that did not migrate. The mean number of GPS locations for the

white-tailed deer dataset was 1,975 per individual. The mean number of GPS locations for the coyote dataset was 1,111 per individual.

During the 2022/2023 winter deer feeder survey flight, 31 feeder locations were identified, spanning both the northern and southern portions of the study area although most ( $n = 27$ ) of the feeders were located in the southern part of the deer wintering area.

During the first winter 2021/2022, snow reached a maximum depth of 56 cm, and the minimum temperature was  $-37.2$  °C. The first autumn migration occurred on December 19 when the snow depth was 2cm and average daily temperature was  $-13.5$ . The first Spring 2022 migration occurred when there was 44 cm of snow, and the temperature was  $-4.4$  °C. During the second winter (2022/ 2023) snow depth reached a max depth of 54 cm and the minimum temperature was  $-40.6$  °C. The first autumn migration occurred on December 16 when the snow depth was 17 cm and average daily temperate was  $-1.7$  °C. The first Spring 2023 migration occurred when there was 22 cm of snow, and the temperature was  $5.4$  °C.

***Time-to-event model of migration***– There was a slight correlation observed between the Snow and NDVI covariates (Winter/Spring 2022,  $r = -0.689$ , Winter/Spring 2023,  $r = -0.656$ ), however the overall condition number of the matrix calculated across all years remained small (less than 3; Supplemental Table 1). This suggests minimal multicollinearity issues, with the condition number below the accepted threshold of 5 (Lazaridis 2007). Therefore, multicollinearity was not considered a significant issue. For three of the four migratory periods studied, the covariate model performed better than

the null model with lower LOOIC values (Table 2). For the Autumn – Winter 2021/2022 migration, there were slightly lower LOOIC values for the no covariate model. The most consistent and certain effect across years and seasons was snow depth. In autumn of both years, deer were more likely to migrate as snow depth increased. Likewise, deer were more likely to migrate in the spring as snow depth decreased. The credible intervals for the effect of snow did not overlap 0 in 3 models, but there was greater uncertainty in the effect during Autumn - Winter 2021/2022. The credible intervals of the temperature and NDVI covariates overlapped 0 throughout all migratory periods, indicating an uncertain effect.

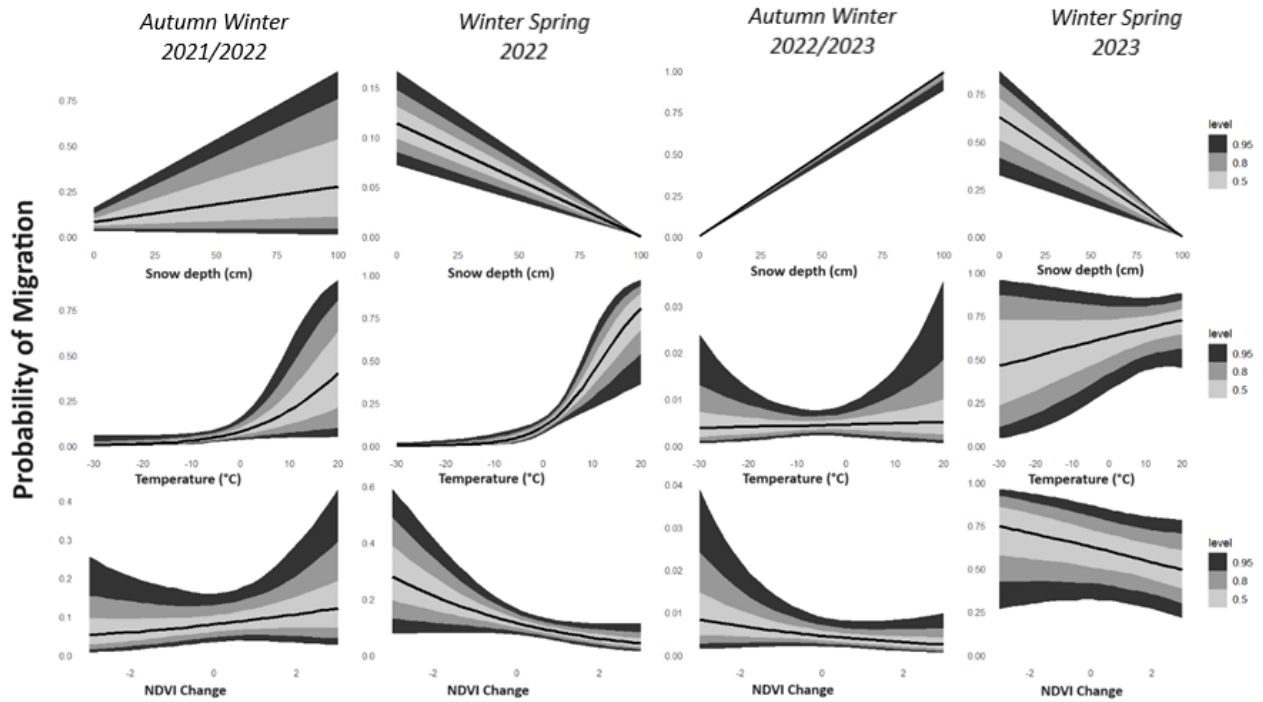
Table 1. Coefficient estimates (coeff.) from  $\beta$  Weibull cure rate time-to-event models fit to global positioning system (GPS) radio collar data from male and female white-tailed deer to assess probability of seasonal migration in south-eastern Ontario, Canada between December 2021, and May 2023. 95% credible limits are shown in parentheses.

Covariate	Coeff. Autumn Winter 2021/2022	Coeff. Winter Spring 2022	Coeff. Autumn Winter 2022/2023	Coeff. Winter Spring 2023
Number of individual deer	37	41	34	58
Snow Depth (cm)	0.269 (-0.333, 0.841)	-1.516 (-2.203, -0.906)	1.003 (0.692, 1.320)	-1.711 (-2.330, -1.128)
Temperature °C	0.222 (-0.316, 0.764)	0.357 (-0.007, 0.760)	-0.311 (-0.792, 0.204)	0.280 (-0.004, 0.562)
NDVI	0.177 (-0.310, 0.733)	-0.418 (-0.826, 0.013)	-0.081 (-0.563, 0.409)	-0.072 (-0.463, 0.335)



Table 2. Leave one out information criterion (LOOIC) for Weibull Cure Rate mixed models assessing the probability of migration, fit to global positioning system (GPS) radio collar data from white-tailed deer, in south-eastern Ontario, Canada between December 2021, and May 2023. LOOIC values were calculated for a covariate model, which included covariates for snow depth, temperature, and normalized difference vegetation index (NDVI) and a null model including no covariates.

Model	Autumn Winter 2021/2022	Winter Spring 2022	Autumn Winter 2022/2023	Winter Spring 2023
Covariate	144.3 (13.5)	225.9 (22.8)	216.1 (19.2)	234.5 (13.8)
Null	137.4 (13.3)	483.6 (12.0)	272.5 (17.0)	340.9 (5.2)



**Figure 2:** The impact of chosen model covariates on the probability of migration.

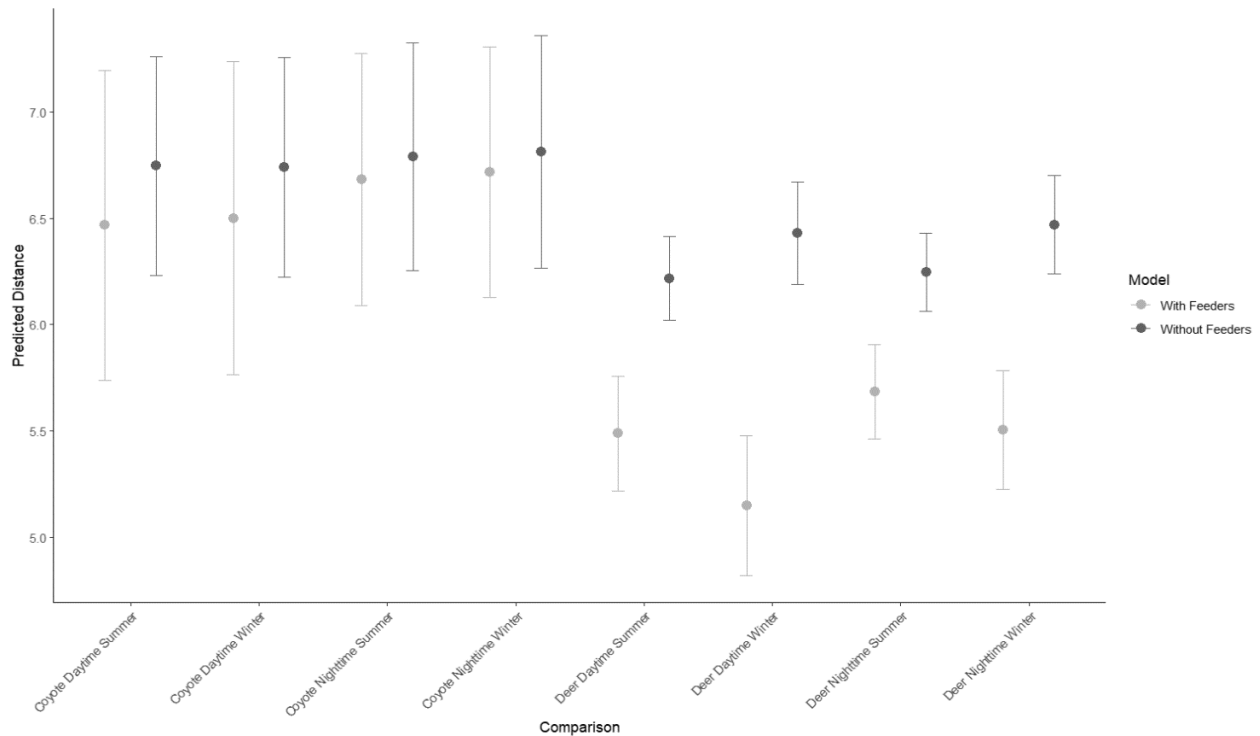
Predicted from Bayesian time-to-event models fit to global positioning system (GPS) radio collar data from white-tailed deer during four distinct seasonal migratory periods, in south-eastern Ontario, Canada between December 2021, and May 2023. Each row corresponds to a different covariate: the top row depicts snow, the middle row temperature, and the bottom row normalized difference vegetation index (NDVI). Color gradient represents predictions at different credible intervals. They show that both NDVI values and temperature effects hold constant at the mean.

**Structure distance and density-** There were significant differences in distances to structures and structure densities between deer and coyotes, with deer being closer (distance  $p < 0.0001$ ; density  $p < 0.0001$ ). For regression models of distance to, and density of structures, we used 181,681 locations from 92 unique deer and 13,335

locations from 12 coyotes. After removing a 1km buffer around each identified supplemental feeding area and removing all deer and coyote locations, we included 90 individual white-tailed deer (109,692 observations) and 12 individual coyotes (11,028 observations).

### **Structure Distance**

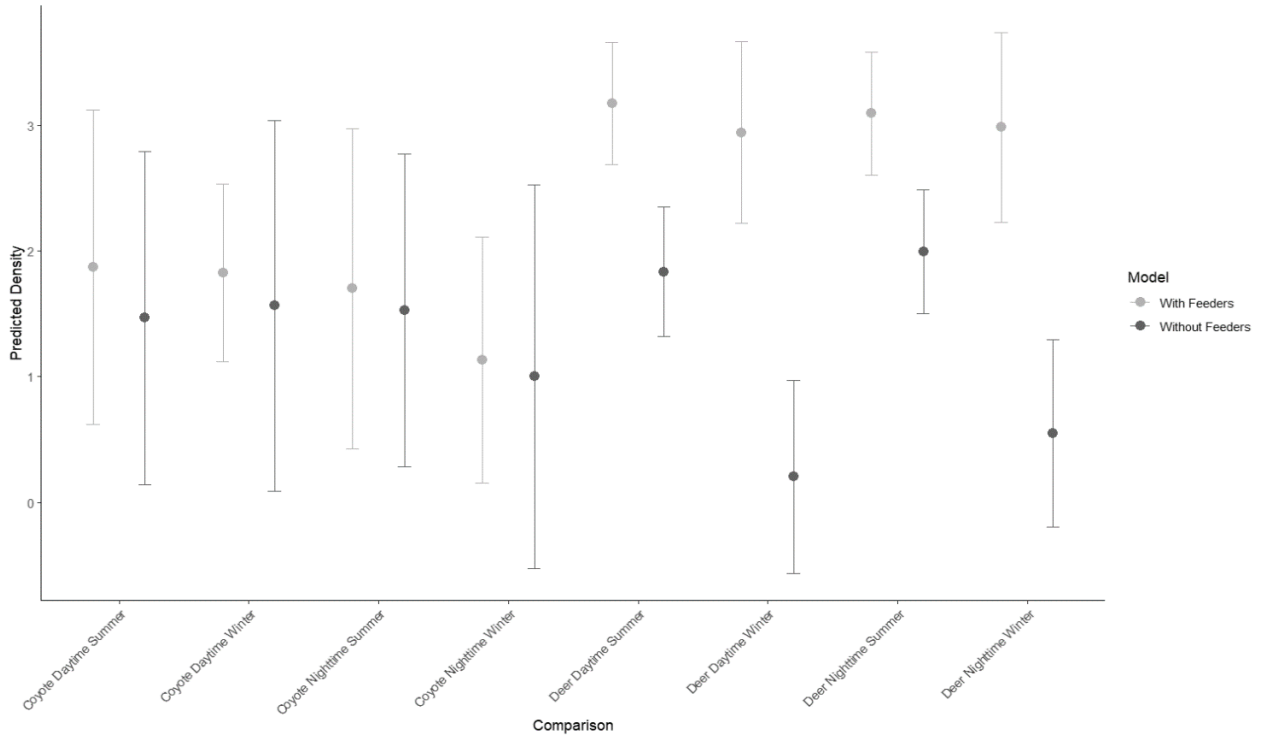
All covariate models had lower AIC values than the corresponding null model (Supplemental Table 6), suggesting the inclusion of covariates better explained the distances to structure and structure densities. For the model with feeder areas included, deer were consistently closer to structures than coyotes (Fig. 3). There was diel and seasonal variation, but this variation was less than that between species and confidence limits of predictions overlapped. Upon filtering the data for locations near feeding sites, the observed effects were diminished, with deer no longer being found to be closer to structures than coyotes (Fig. 3).



**Figure 3:** Predicted distances in log<sub>10</sub>[meters], to human structures for different day time, seasonal and species combinations from general linear mixed effect models (GLMM) fit to global positioning system (GPS) radio collared data from white-tailed deer and Coyotes, in south-eastern Ontario, Canada between December 2021, and May 2023. Shown with 95% confidence intervals.

### Structure Density (GLMER Model)

Deer used areas with higher densities of structure than coyotes at all times of year and between day and night (Fig. 4). Upon filtering the data for locations near identified feeding sites, the results diminished again, with no observed differences between deer and coyote habitat use for structure density at all times of year and between day and night (Fig. 4) .



**Figure 4:** Predicted structure density in  $\log_{10} \pi(1\text{km})^2$  for different day time, seasonal and species combinations from general linear mixed effect models (GLMM) fit to global positioning system (GPS) radio collared data from white-tailed deer and coyotes, in south-eastern Ontario, Canada between December 2021, and May 2023. Shown with 95% confidence intervals.

## Discussion

Animal migrations play a crucial role in transporting nutrients and connecting landscapes (Bauer and Hoye 2014). Determining the factor's influencing migration is critical for assessing the drivers of ecosystem dynamics. To understand the proximate drivers of deer migration, we looked at four migratory seasons of data during a two-year study (Fall 2021 to Spring 2023), first focusing on the environmental stimuli initially triggering deer to leave for their winter range in autumn and for their return migration in spring. We then examined differences in habitat use between seasonal ranges, focusing on whether deer and coyotes influenced each other's habitat use. Ultimately, we were interested in whether deer migrated to alleviate predation risk through a de facto *human shield*, or in response food availability.

### Driver of migration timing

Snow depth had the most consistent influence in determining migration timing across models. Coefficients for snow depth were credible, or nearly so, in all models. In autumn, most deer migrated after snow had reached nearly 50 cm (95% of deer migrated after 48 cm in 2021 and 45 cm in 2022). At this depth, we presume that snow began to limit movement, likely cueing deer to move south. During the return spring migration, the effect of snow was reversed, with deer moving once snow melted to a certain level. These results are consistent with existing studies that show that ungulate predation rates increase with increasing snow depth in the autumn and that deep snow forces competition for forage of lower quality at greater energy expense (Dumont et al. 2005, Hoskinson and Mech, 1976, Nelson and Mech 1986, DeGiudice et al. 2002, Olsen et al. 2021). Likewise, loss of snow cover in the spring has been shown to initiate

return migrations to summering areas (Nelson, 1995). Deer that migrate, may be able to access conditions that buffer the effects of snow, and potentially reduce predation risk, while accessing higher quality food. In the spring, it was even more apparent that deer waited for snowpack to melt to levels less than what initiated autumn migration before migrating back to their northern range. During the Spring 2022 migration, 95% of deer migrated after there was 4cm or less of snow and 18cm or less in Spring 2023. In Spring 2023 we observed a delay in snow melt as the migratory period extended further into April than the Spring 2022 period. Despite the delayed onset, 80% of individuals still waited until there was 7cm of snow or less. The loss of this snow cover in the spring could also act as a cue to signal access to higher quality browse and prevent any mobility issues, as migration itself is inherently risky (Hebblewhite and Merrill, 2009). The other covariates that we examined in our models had inconsistent and uncertain effects across years. We found that most individuals migrated out of sync with the peak in spring green in contrast to the forage maturation hypothesis (Bischoff et al. 2012) and that plant biomass levels did not influence the timing of migrations. Likewise, temperature showed considerable variability across years and seemed unrelated to migration.

### **Human Shield or Food?**

Whether our deer migrated because of food or to mitigate predation risk, the timing of migration should, on average, provide them with the greatest overall fitness benefit. The results from our time-to-event analysis showed that snow had the greatest proximate impact on the onset of migration. We then attempted to further assess the relative influence of predation on the ultimate causes of migration due to the established

links between snow depth and a deer's vulnerability to predation (Nelson and Mech 1986; Patterson and Messier 2000). During the first winter of collaring, we noted that large numbers of people living within the wintering area were providing substantial quantities of supplemental feed to deer. This allowed the opportunity to conduct analyses with and without deer and coyote locations near feeders to concurrently assess the relative influences of food and predator shielding. Specifically, we predicted that if shielding from predators was the primary reason for deer migration, then we should see consistent patterns of deer being closer to and in areas with higher density of human structures regardless of the presence of supplemental feeding. In contrast, if deer were primarily migrating to access this supplemental feed (food driven), then we predicted that deer would be closer to and in areas of greater human structure density only in the models including areas close to supplemental feeding.

In models of distance to structure that included areas with supplemental feed, deer were always closer to structures regardless of time of day or season (Fig. 3). The effect of species in the model showed that deer clearly were choosing to be closer to human structures than coyotes. After filtering for supplemental feeding locations, this effect changed substantially. Deer were still predicted to be closer to structures than coyotes in most instances, but confidence intervals overlapped and there was a clear shift whereby deer were much further from structures that did not have supplemental feed. The same trend was apparent when measuring structure density (Fig. 4).

In a habitat use process favouring the *human shield*, we would have expected to observe differences between coyotes and deer regardless of the presence of supplemental food. Coyote activity patterns peak at night and the early morning



(Patterson et al. 1999, Grinder and Krausman, 2001). Deer may alter their temporal activity patterns in the presence of predators to reduce the chance of adverse consequences (Cherry et al. 2015, Higdon et al. 2019). Although deer tended to be attracted to a higher density of structures, this effect changed drastically once we filtered out locations within 1 km of known supplemental feeding. Given this change in effect, our results do not support the human shield hypothesis, but rather a food driven migration emphasized by the strong effect that supplemental feeders are having on winter habitat use. However, the finding that coyotes continued to select for locations in similar proximity to human structures, regardless of the presence of feeding suggests they may be cuing in on developed areas as a proxy for deer presence. A similar pattern was observed in northern Ontario where wolves selected habitat preferred by moose (their primary prey), more strongly than they responded to actual moose locations at any specific point in time (Kittle et al. 2017). The rural-urban wintering habitat in our study area is also not consistent with what constitutes classic white-tailed deer wintering habitat (Rongstad and Tester, 1969, Morrison et al. 2003). The core wintering area would be described as being devoid of natural food with an absence of mature softwood canopy cover, thereby exposing deer to the varied environmental conditions that cued them to leave their autumn range.

Although our results do not support the human shield hypothesis with respect to use of winter habitat by deer, we can't exclude the established effect that predation has on the onset of migration. The aggregation of deer during winter yarding facilitates collective benefits; it creates a dilution effect from predators and deer create communal trails which increase their mobility (Nelson and Mech, 1981, Parker et al. 1984, Messier

and Barrette, 1985). Ultimately, the link between a snow induced migration and habitat use based on food availability, likely involves a combination of an immediate response to the increased risk of predation and a longer-term response to exploit food resources, maximising the deer's overall fitness.

### **Management Implications**

The strongest driver of the timing of migration was snow depth; wildlife managers will need to consider the potential effect that climate change may have on snowfall levels and ultimately on the timing and extent of deer migrations. Climate change leading to lessened snow depth might lead to a loss in migratory behaviours by deer. Furthermore, in systems heavily impacted by anthropogenic activities, conservation efforts will need to address the increase in deer- human conflict and potential for disease spread through unnaturally high congregations surrounding supplemental feeders.

### Chapter 3: Conclusion

Current literature on migratory behaviours of white-tailed deer primarily focuses on the external environmental factors that influence the timing of their departures (Sabine et al. 2002, Fieberg et al 2008, Grovenburg et al. 2009). Here, we attempted to explore whether predation risk or access to food were stronger ultimate drivers of migration. Our study area provided a unique opportunity to observe the variation in migration strategies of a northern white-tailed deer population, within a landscape shaped by human presence. Our results suggest that deer selected for habitats that supplied sufficient food, as opposed to habitat that provided a predator mitigation benefit.

Our results support existing literature showing snow is the primary driver of white-tailed deer migration timing (Brinkman et al. 2005, Nelson 1998, Fieberg et al, 2008). Deer consistently responded to increasing and disappearance of snow, though there were differences between seasons. Deer during the spring migrated when less snow (4cm in 2022 and 18cm in 2023) was left on the ground than in the autumn (48cm in 2021 and 45cm in 2022). This result was consistent with other findings in the literature. Nelson et al. 2004 found that deer migrated in the spring when there was less than 9 cm of snow and between 9-24 cm of snow in the autumn. One possible explanation is that deer have a better body condition in the autumn than in the spring after a long winter of experiencing adverse environmental conditions (Nelson 1995). Deer that are in better condition in the autumn period, would have an easier time navigating through snow and possibly tolerate less food without the expense of survival. In the spring, when deer are run down and in poor body condition, they may have to

wait longer to migrate under more favourable conditions, when there is less snow to impede their movements and provide better access to ground forage (food driven hypothesis). Thus, this explanation further aligns our food driven suggested hypotheses. Of note, when studying animal behaviour, observing changes in long-term studies is paramount to improving our understanding of said behaviours, especially when looking at seasonally variable environmental variables. Thus, a limitation in this study is its short duration, when considering the annual variation in winter severity and spring plant biomass.

Deer are adaptable, resilient, and their population density and range is increasing in response to human development and climate change (Weiskopf et al. 2019). During migrations, human impacted areas would not normally be characterized as suitable habitat (Morrison et al. 2003, Hurst and Porter, 2008). However, humans may alter environments such that conditions are amenable to migrating individuals (Kilpatrick and Spohr, 2000, Berger 2007). We found evidence suggesting that deer relied on human altered habitats for food. Deer selected for habitat closer to and in higher density of structures than coyotes did during the winter, but this effect disappeared when removing locations near supplemental feeding, indicating the presence of humans alone was not driving the difference in habitat use between species. Our results showcase that deer were willing to adjust their behaviours in response to the availability of supplemental feed. After filtering supplemental feeding locations, the strength of differences in habitat use between coyotes and deer diminished. In these remaining areas, deer and coyotes treated structures similarly when supplemental food was not present. This reinforces

that deer migrations were more likely food driven and the findings preclude the existence of a simultaneous predator buffer.

Another emerging issue deer managers across North America are facing is the threat of infectious disease, primarily chronic wasting disease (CWD). The rate of CWD spread can be strongly influenced by migrations (Edmunds et al. 2018, Conner and Miller 2004). Disease transmissibility also becomes a concern when deer are congregating in higher-than-normal densities (Jennelle et al. 2014). Circumstances that allow for these conditions include human activities such as baiting for hunting purposes, supplemental backyard feeding for viewing, and naturally occurring winter deer yards (Messier and Barrette, 1985, Thompson et al. 2008). The heavy congregations driven by supplemental feed, paired with the subsequent migration to sometimes distant locations suggest the strong potential for feeding and migration to contribute to rapid spread of CWD and other diseases. The banning of activities that promote these circumstances is one of the first tools wildlife managers use when trying to address disease concerns or reduce the spread of a disease (Mysterud et al. 2023). Such bans may cause further changes and impacts on migratory patterns of deer; factors that wildlife managers must consider when determining a response to an outbreak.

Migrations are an adaptive strategy, but ungulate migration routes are being disrupted by human activities (Bolger et al. 2008, Harris et al. 2009, Lendrum et al. 2014). Given our results, wildlife managers must consider the potential future impacts of human development and activity on the migratory behaviours of white-tailed deer and the resulting impacts on their population dynamics. Human activity such as sport hunting, has been shown to impact elk migrations, resulting in them staying within

protected areas longer than historically recorded (Barmore, 2003). Predation risk in wolf-ungulate systems, has also been shown to force ungulates to migrate out of core wolf ranges in an attempt to reduce mortality risk (Mech, 1977). In the present day when the loss and alteration of wildlife migrations has already been recognized by wildlife researchers, determining the cues that influence these movements and their ultimate causes, may provide a mechanism for their future restoration (Ripple and Beschta, 2004).

Although white-tailed deer are known to be adaptable, we cannot discount the ability for human development to disrupt long learned migratory behaviours. We live in a precarious time where the impacts of human activities are ever increasing, and many animal behaviours are being disrupted. Our findings underscore the need for wildlife researchers to continue to observe animal behaviours throughout this period, and employ adaptive management techniques, before critical life history processes are altered or lost forever.

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## Supplemental

Table 1. Pearson correlation coefficients for the variables used in our time-to-event analysis assessing the drivers of migration of white-tailed deer, in south-eastern Ontario, Canada between December 2021, and May 2023. Each migratory period observed in our study is shown.

Covariate	Autumn Winter 2021/2022	Winter Spring 2022	Autumn Winter 2022/2023	Winter Spring 2023
Snow Depth: Temperature	-0.571	-0.192	-0.304	-0.564
Snow Depth: NDVI	-0.252	-0.689	-0.574	-0.656
Temperature: NDVI	-0.029	-0.289	0.300	0.335
<i>Condition Number</i>	2.10	2.46	2.06	2.69

Table 2. Coefficient estimates (Est.), standard errors (SE) and 95% confidence limits from models fit to data on the on distance to structures from GPS radio collar locations of coyotes and white-tailed deer, in south-eastern Ontario, Canada between December 2021, and May 2023. Species: Coyote =0, Deer= 1. Season: Summer Range = 0, Winter Range = 1. Day\_night: Daytime = 0, Nighttime = 1.

<i>Fixed Effect:</i>	<b>Est</b>	<b>SE</b>	<b>2.5%</b>	<b>97.5%</b>
<i>(Intercept)</i>	6.467	0.371	5.739	7.194
<i>Species</i>	-0.979	0.396	-1.753	-0.203
<i>Season</i>	0.033	0.268	-0.492	0.558
<i>day_night</i>	0.214	0.094	0.0299	0.397
<i>Species:Season</i>	-0.372	0.304	-0.967	0.224
<i>Species:day_night</i>	-0.018	0.102	-0.217	0.181
<i>Season: day_night</i>	0.003	0.062	-0.119	0.124
<i>Species:Season:day_night</i>	0.157	0.080	0.7x10-3	0.314

Table 3. Coefficient estimates (Est.), standard errors (SE) and 95% confidence limits from models fit to data on the on distance to structures with feeding areas removed, from GPS radio collar locations of coyotes and white-tailed deer, in south-eastern Ontario, Canada between December 2021, and May 2023. Species: Coyote =0, Deer= 1. Season: Summer Range = 0, Winter Range = 1. Day\_night: Daytime = 0, Nighttime = 1.

<i>Fixed Effect:</i>	<b>Est</b>	<b>SE</b>	<b>2.5%</b>	<b>97.5%</b>
<i>(Intercept)</i>	6.746	0.262	6.232	7.259
<i>Species</i>	-0.529	0.281	-1.079	0.021
<i>Season</i>	-0.008	0.034	-0.074	0.059
<i>day_night</i>	0.041	0.031	-0.020	0.102
<i>Species:Season</i>	0.220	0.129	-0.034	0.473
<i>Species:day_night</i>	-0.011	0.041	-0.092	0.069
<i>Season: day_night</i>	0.033	0.047	-0.060	0.125
<i>Species:Season:day_night</i>	-0.023	0.062	-0.144	0.097

Table 4. Coefficient estimates (Est.), standard errors (SE) and 95% confidence limits from models fit to data on the structure density from GPS radio collar locations of coyotes and white-tailed deer, in south-eastern Ontario, Canada between December 2021, and May 2023. Species: Coyote =0, Deer= 1. Season: Summer Range = 0, Winter Range = 1. Day\_night: Daytime = 0, Nighttime = 1.

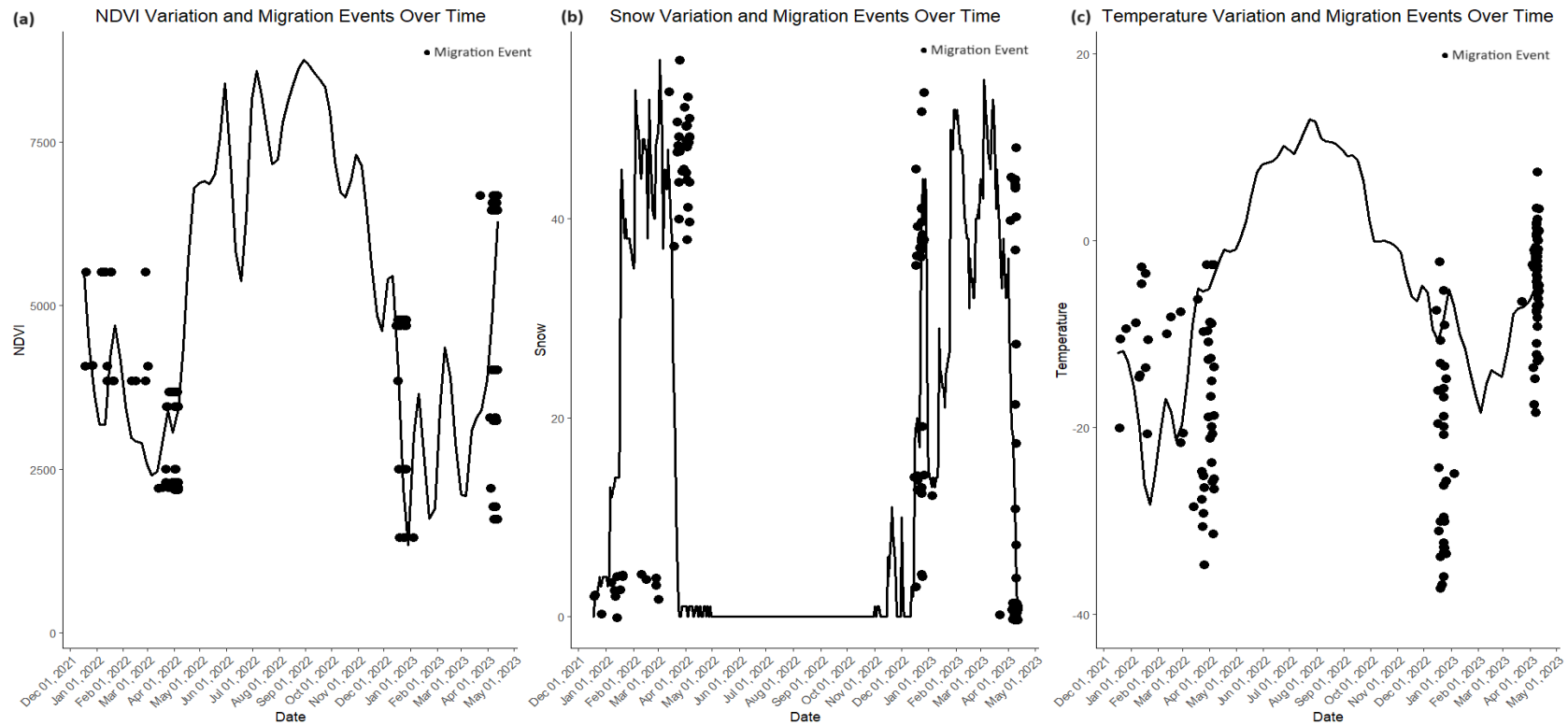
Fixed Effect:	Est	SE	2.5%	97.5%
(Intercept)	1.873	0.639	0.621	3.125
Species	1.302	0.685	-0.040	2.645
Season	-0.047	0.364	-0.760	0.666
day_night	-0.171	0.118	-0.401	0.060
Species:Season	-0.185	0.531	-1.227	0.856
Species:day_night	0.092	0.125	-0.153	0.337
Season: day_night	-0.521	0.188	-0.888	-0.153
Species:Season:day_night	0.642	0.200	0.250	1.035

Table 5. Coefficient estimates (Est.), standard errors (SE) and 95% confidence limits from models fit to data on the structure density with feeding areas removed, from GPS radio collar locations of coyotes and white-tailed deer, in south-eastern Ontario, Canada between December 2021, and May 2023. Species: Coyote =0, Deer= 1. Season: Summer Range = 0, Winter Range = 1. Day\_night: Daytime = 0, Nighttime = 1.

<i>Fixed Effect:</i>	<b>Est</b>	<b>SE</b>	<b>2.5%</b>	<b>97.5%</b>
<i>(Intercept)</i>	1.467	0.678	0.490	3.149
<i>Species</i>	0.368	0.727	-1.416	1.435
<i>Season</i>	0.098	0.249	-0.717	0.868
<i>day_night</i>	0.060	0.176	-0.443	0.215
<i>Species:Season</i>	-1.732	0.505	-2.688	-0.346
<i>Species:day_night</i>	0.100	0.191	-0.083	0.639
<i>Season: day_night</i>	-0.626	0.396	-1.202	-0.076
<i>Species:Season:day_night</i>	0.813	0.416	0.248	1.490

Table 6. Candidate general linear mixed effect models (GLMM) to investigate variation in the densities and distances to structures by white-tailed deer and coyotes, between feeding and non-feeding areas, in south-eastern Ontario, Canada between December 2021, and May 2023. Individual animals were included as a random effect. Akaike Information Criterion (AIC) comparison for GLMM mixed models showing results for covariate vs null model.

<i>Model</i>	<b>LMER (With feeders)</b>	<b>GLMR (With feeders)</b>	<b>LMER (Without Feeders)</b>	<b>(GLMR Without Feeders)</b>
<i>AIC</i>	544464	5977878	255178	1603862
<i>AIC Null</i>	571574	6905006	269687	1806063
<i>ΔAIC</i>	27109	926128	14509	202201



**Figure 1:** Temporal dynamics between environmental factors and migration events observed in our study area, in south-eastern Ontario, Canada between December 2021, and May 2023. The left plot (a) displays the normalized difference vegetation Index (NDVI) over time, showing vegetation changes. NDVI values (which normally fall between -1.0 and 1.0) are scaled by 10,000. The middle plot (b) illustrates the variation in snow depth (cm). The bottom plot (c) exhibits the fluctuations in temperature ( $^{\circ}\text{C}$ ). In each plot, black points denote migration events.