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Abstract:

The outcome of encounters between predators and prey affects predation rates and ultimately population dynamics. Determining how environmental features influence predation rates helps guide conservation and management efforts. We studied where gray wolves (*Canis lupus* (Linnaeus, 1758)) and coyotes (*Canis latrans* (Say 1823)) killed white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) in northern Wisconsin, USA. We monitored 499 white-tailed deer for cause-specific mortality between 2011-2014 using VHF radio collars. We investigated the locations of 125 deer mortalities, and determined 63 were canid (wolf or coyote) kill sites. We analyzed spatial patterns of kill sites using resource selection functions (RSF's) in a model selection framework, incorporating environmental variables including vegetative cover, human development, snow depth, and water. We found no evidence that vegetative cover or human development affected predation risk; however we did find that increasing snow depth resulted in increased relative predation risk. This finding is consistent with existing research on the influence of snow cover on white-tailed deer survival. Our results suggest that understanding the spatial and temporal patterns of white-tailed deer predation requires a better understanding of snow depth variation in space and time. As climate change scenarios predict changes in snowfall throughout the Northern Hemisphere, understanding the effect on predator-prey spatial dynamics will be important for management and conservation efforts.

Keywords: Predation, white-tailed deer, *Odocoileus virginianus*, gray wolf, *Canis lupus*, coyote, *Canis latrans*, predator-prey dynamics, seasonal variation, spatial dynamics

Introduction

Animals make behavioral tradeoffs to increase survival (Boyce and McDonald 1999; Kunkel and Pletscher 2000), and ultimately fitness (DeCesare et al. 2014). Prey animals balance foraging and vigilance behaviors to meet daily energy requirements while also avoiding exposure to predators. Conversely, predators maximize hunting efficiency by selecting for areas with more prey (Sih 2005). These opposing strategies can be affected by biotic and abiotic conditions within an animal's environment (Lima et al. 2002). For example, some environments expose prey to greater predation risk (Hebblewhite et al. 2005a), which may influence spatially explicit population growth (DeCesare et al. 2014).

Landscape features and vegetation may affect predator and prey encounters, as well as the outcome (Lima and Dill 1990; Kunkel and Pletscher 2000; Hebblewhite et al. 2005a; Kauffman et al. 2007). For example, elevational gradients associated with variation in forest composition, structure, and microclimates can change the distribution of prey and where predators seek them (Kunkel and Pletscher 2000). Vegetative cover may be avoided by prey species when it harbors predators (Underwood 1982). Where there is human development, anthropogenic linear features can increase search efficiency of cursorial carnivores while hunting prey, thus increasing predation rates (Dickie et al. 2017; Newton et al. 2017). However, because large carnivores are sensitive to human presence (Wilmers et al. 2013), human activity may actually alter predator and prey spatial dynamics (Hebblewhite et al. 2005b; Muhly et al. 2011; Zimmermann et al. 2014). For example, white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) may select for wintering areas associated with human activity, which reduces their risk of predation from wolves (*Canis lupus* (Linnaeus, 1758)) (Hoskinson and Mech 1976).

Determining the influence of landscape features on the outcomes of predator and prey encounters is important for conservation planning and wildlife management efforts (Newton et al. 2017).

Seasonal variability can change the abiotic conditions as well as the availability of food and water within landscapes, thus affecting the behaviors of predators and prey (Nelson and Mech 1986; de Boer et al. 2010; Allen et al. 2014). For instance the amount, timing, and duration of snow cover can affect predation risk (Hebblewhite 2005) and trophic interactions (Penczykowski et al. 2017). For example, snow depth has been positively associated with the kill rate of wolves on both elk (*Cervus elaphus* (Linnaeus, 1758)) (Hebblewhite 2005) and white-tailed deer (Nelson and Mech 1986). When deciduous trees drop their leaves the thermal environment changes, and coniferous forest provides thermal cover that may be favored by prey species (Ozoga 1968). Prey species may also alter their movement patterns in response to seasonal changes in environmental factors, both to maximize forage intake and reduce predation risk (Gilbert et al. 2017).

Prey species often make foraging tradeoffs to meet daily energy requirements. For example, caribou (*Rangifer tarandus* (Linnaeus, 1758)) selected for less nutritious forage to reduce exposure to predation from wolves (Ferguson et al. 1988). Many ungulates migrate; a tradeoff where costly seasonal range movement is outweighed by the benefits provided by wintering habitat, including refuge from predators (Hoskinson and Mech 1976; Hebblewhite and Merrill 2009). While the importance of seasonal variability on the functional and numeric responses of prey populations has been well studied (Lima et al. 2002; Hebblewhite 2005; Vucetich et al. 2011), the effect of seasonal variability on the outcome of predator-prey spatial dynamics has not been well studied but may increase our understanding of fine-scale population dynamics (Kautz et al. 2020).

Improved understanding of the relationship between large carnivores and their prey has improved management strategies (Mech et al. 2000) and increased support for conservation efforts (Ripple et al. 2014). Management of white-tailed deer and predator populations is controversial. Although regulated harvest of white-tailed deer is the highest source of deer mortality, non-hunting mortality may be more important in population modeling and monitoring of deer (Halls 1984; Norton 2015). Despite public controversy over the impact of predators on Wisconsin's white-tailed deer population, there is little research to suggest that wolves or coyotes (*Canis latrans* (Say, 1823)) are having a substantial impact on white-tailed deer populations at large spatial scales (Norton 2015). One way to explain this discrepancy is that coyotes and wolves impact the population growth or behavior of white-tailed deer at a smaller spatial scale. Elucidating small-scale spatial variation in white-tailed deer survival may allow insight into fine-scale numeric or behavioral impacts affecting population growth (DeCesare et al. 2014).

Our objective was to understand the environmental factors influencing canid predation on white-tailed deer in northern Wisconsin. We analyzed predation from two canids: coyotes and wolves, because they share similar hunting strategies as cursorial predators that are adapted to run down prey, and hunt in packs (Creel et al. 2013). We hypothesized that white-tailed deer risk of mortality would increase with increasing linear features (Newton et al. 2017), closer proximity to wolf packs (Mech 1977), and greater snow depth (Nelson and Mech 1986; Hebblewhite 2005). We hypothesized that mortality risk would decrease with increasing human development (Hebblewhite et al. 2005b; Wang et al. 2015), agriculture (Muhly et al. 2011), and coniferous cover (Ozoga 1968; Nelson and Mech 1981; Delgiudice et al. 2013). Because population dynamics may vary at small spatial scales, understanding the relative impact of environmental

factors on the outcome of white-tailed deer encounters with canids may be important for justifying landscape and wildlife management.

Materials and methods

Study Area

Our study area was within the Deer Management Units (DMU) of Ashland, Rusk, and Sawyer counties in northern Wisconsin, USA (Figure 1). The area contains similar proportions of public land (49%) and private land (51%). The landscape and vegetation was shaped by the last glacial period, where receding glaciers deposited soils for the foundation of forest communities throughout the region (Curtis 1959). The study area was mainly forested (80%) with northern hardwoods and softwoods including sugar maple (*Acer saccharum* (M., 1785)), American beech (*Fagus grandifolia* Ehrh.), American basswood (*Tilia Americana* L.), white ash (*Fraxinus Americana* L.), northern red oak (*Quercus rubra* L.), quaking aspen (*Populus tremuloides* Michx.), yellow birch (*Betula alleghaniensis* Britton), and eastern hemlock (*Tsuga canadensis* Carrière 1855) (Curtis 1959). The carnivore guild in this system included black bears (*Ursus americanus* (Pallas, 1780)), bobcats (*Lynx rufus* (Schreber, 1777)), gray wolf, coyotes, red fox (*Vulpes Vulpes* (Linnaeus, 1758)), and gray fox (*Urocyon cinereoargenteus* (Schreber, 1775)). The climate throughout the study area can be classified by cold winters and warm, humid summers (Curtis 1959).

Field Methods

We captured white-tailed deer during the winters of 2011-2014 using Clover netted-cage traps (Clover 1956), Stephenson box traps (Rongstad and McCabe 1984), modified rocket nets (Kiwi Captures International, Waukesha, WI, USA), modified drop nets (Ramsey 1968), dart

guns, and helicopter net-gunning (Barrett et al. 1982; Breton and Potvin 1988) across 268 unique trapping sites that were >100 m apart during the winters (December-April) of 2011-2014 (Norton 2015). Adult white-tailed deer were aged to three discrete age classes (6-10 months old, 18-22 months old, and >30 months old) using tooth wear and replacement techniques (Severinghaus 1949). Adult white-tailed deer (> 6 mo) were monitored using VHF radiocollars (Advanced Telemetry Systems, Inc., Isanti, MN, USA). Adult males were collared each year of the study while adult females were radio collared in 2012 and 2014. In 2014, juvenile females were also radio collared. White-tailed deer captured by search crews during a concurrent fawn recruitment study (Warbington et al. 2017) that survived to January were also monitored for this study. All white-tailed deer were administered a pair of uniquely numbered metal ear tags imprinted with contact information for the Wisconsin Department of Natural Resources (Ketchum Mfg. Co, Inc., Lake Luzerne, New York, USA). Animals were handled in accordance with the University of Wisconsin Animal Care and Use Committee (Research Animal Resources Center, protocol number A01446).

VHF collared white-tailed deer were monitored for survival 1-3 times per week. Locations of radio collared white-tailed deer were estimated one time per week using the intersection of at least two telemetry azimuths or by visual observations. Location estimates were confirmed by field technicians using projected locations overlaid on aerial imagery. The VHF collars transmitted a mortality signal upon lack of movement for six hours. When a mortality signal was detected, the collar was located as soon as possible (generally < 7 days). Upon recovery of the collar, the mortality location (based on carcass remains) was marked using a handheld GPS unit, followed by a thorough investigation of the area (≤ 100 meters) surrounding the collar to find predator specific sign such as scat, tracks, hair, cache, trails, bed sites, and dens.

Hunter and human activity was noted along with documentation of general habitat characteristics. Field necropsy of the carcass was conducted when possible. In certain cases we submitted carcasses to the University of Wisconsin-Madison Veterinary Diagnostic Laboratory or the WI DNR Animal Diagnostics Laboratory for necropsy by a veterinarian pathologist. In cases where cause of death wasn't evident, detailed photographs of carcasses and sign were taken and examined by multiple wildlife biologists and veterinarians to determine cause-specific mortality.

Model Covariates

Predation is a process that takes place over multiple behavioral stages including encounter, attack, and kill (Hebblewhite et al. 2005a). Therefore, inferring spatial patterns of white-tailed deer mortality may be limited based on attributes in the immediate vicinity of carcass or mortality locations. We buffered locations of deer mortalities by a 300 m radius (hereafter, kill sites) to approximate a scale at which all stages of canid predation may occur (Ozoga and Harger 1966; Nelson and Mech 1981; Paquet 1992). We used the same buffer for wolves and coyotes because chase distances between encounter-kill are generally the same (Paquet 1992). We quantified spatial variables including developed, agriculture, coniferous forest, broad leaf, and broad leafed deciduous/mixed forest (Table 1) within kill sites using spatial data layers in ArcGIS (Esri 2014) and Geospatial Modeling Environment (Beyer 2009).

We calculated proportions of categorical land cover and vegetative characteristics at each kill site from 'Wisland 2.0', which is a Wisconsin land cover dataset generated from classified aerial land cover images from 2010-2014 (Wisconsin Department of Natural Resources 2016). Wisland 2.0 contains four hierarchical land cover classifications at a 30 m resolution. Level 1 is

the most generalized classification (ex., “forest”, “developed”, “open water”) where level 4 contains the highest level of classification detail (ex., “red oak”, “jack pine”, “sugar maple”). Classification accuracy generally decreases with each level, thus, we calculated land cover data using classification levels 2 and 3 which provide an overall accuracy of 86%, and 73%, respectively. We combined land cover classifications to spatially relevant categories of developed, agriculture, coniferous forest, broad leaf, and broad leafed deciduous/mixed forest (Table 1).

Linear features created naturally and through human development may affect predator and prey dynamics (Dickie et al. 2017; Newton et al. 2017). We estimated natural and anthropogenic linear features by calculating edge and road length within kill sites. We created line shapefiles from Wiscland 2.0 where two unique level 1 land cover categories met. We then calculated the linear amount of edge within each kill site. In a similar fashion, we calculated the linear amount of roads within kill sites using 2014 TIGER line files (2010). We considered non-arterial roads for their potential to increase the search efficiency of cursorial canids (Newton et al. 2017) which included minor paved roads to trails and walking paths restricted to vehicular traffic (TIGER classification codes S1400, S1500, S1640, S1710, S1740, S1820).

We collected daily snow depth data each year of the study for 1 November through 31 April using data from the Midwestern Regional Climate Center that was measured at a weather station within the study area (Winter, WI, USA). For days with missing snow depth measurements, we used snow depth from the nearest previous measurement (which was generally less than one or two days). We calculated the average snow depth from within 7 days prior to the date the carcass was located because this represented the longest amount of time possible between receiving a VHF mortality signal and a carcass investigation.

Wolf territories affect the distribution and habitat use of white-tailed deer (Mech 1977) as well as the distribution of sympatric coyotes (Switalski 2013). The Wisconsin Department of Natural Resources estimates wolf pack territories through multiple methods based on winter track surveys, mortalities, depredations, reported observations, and through radiolocations of collared individuals (Wydeven et al. 2009). We calculated the distance from kill sites to wolf territory centers as a relative measure of risk for white-tailed deer because 1) territory centers are likely a better measure of wolf presence than territory boundaries in saturated wolf populations because they are more stable over time (Mech and Boitani 2003; Mladenoff et al. 2009) and 2) within wolf territories, predation on white-tailed deer occurs first at the center then towards the outside of the territory boundary (Mech 1977). We estimated the geometric center of wolf pack territories for each year of the study using shapefiles provided by the Wisconsin Department of Natural Resources (WDNR).

Statistical Analyses

We evaluated spatial patterns in kill sites using resource selection functions (Manly et al. 2002; Keating and Cherry 2004). An RSF evaluates patterns of used, unused, or available resource units for an animal, and resources used disproportionately relative to their availability are considered selected by that animal (Boyce et al. 2002). We evaluated spatial patterns in kill sites using two RSF sampling designs (Manly et al. 2002; Keating and Cherry 2004). First, we compared used and *unused* resource units (hereafter, UU method; *i.e.*, sampling Protocol C, Design III; Manly et al. 2002). Under this design, kill site locations were compared to the VHF relocations from when the individual deer was alive. In this instance we assumed kill sites and VHF relocations to be discrete (*i.e.*, no contamination), therefore can be considered a case-control design (Keating and Cherry 2004).

For our other sampling design, we compared used and *available* resource units (hereafter, UA; sampling Protocol A, Design I; Manly et al. 2002). Under the UA design, kill sites were compared to random locations. Ten random locations per kill site were selected within an estimated white-tailed deer home range (Stewart et al. 2011) of each kill site using a donut-shaped buffer of radius 600-1200 m from a bivariate uniform distribution using Geospatial Modeling Environment (Beyer 2009). We used a 600 m inner buffer constraint to prevent overlap between kill sites and random locations (*i.e.*, pseudoreplication). We assigned each random location a random day within the year during which the paired kill site occurred to calculate snow depth. This design differs from the UU design because we did not make the assumption that kill sites and random locations were discrete (*i.e.*, possible contamination).

Statistical modeling was performed using program R (R Core Team 2018). For each sampling design we developed our RSF using a generalized linear model with a logit-link function where the observed response follows a binomial distribution, and explanatory variables ($x_1, x_2, \dots, x_p$) are measured on the sample of used, unused, and available resource units (Manly et al. 2002). These models estimate the conditional probability of use ($P(y=1 | x_1, x_2, \dots, x_p)$), and can be interpreted as relative risk (Keating and Cherry 2004). We did not include random effects for individual animals (Gillies et al. 2006) because the number of locations per individual animal was prohibitively low in the UU design and because it was considered unnecessary under balanced sampling designs and when animals respond to resources in a similar way (Gillies et al. 2006).

We developed a set of 12 *a priori* models nested within a global model representing biologically plausible combinations of our fixed effects (Distance to wolf pack territory center, developed, agriculture, coniferous forest, broad leaf deciduous/mixed forest, open water, roads,

edge, snow depth; Table 2). Prior to model fitting we assessed collinearity between all fixed variables, excluding variables which had a correlation coefficient $r \geq 0.70$ or whose correlations were biologically feasible (Burnham and Anderson 2002). We compared models using Akaike's Information Criterion (AIC) (Burnham and Anderson 2002) in the R package MuMIn (Bartón 2016). We selected competing models using ΔAIC , considering any model with a $\Delta AIC < 2$ to have substantial support and with $\Delta AIC < 4$ to be biologically relevant (Burnham and Anderson 2002; Allen et al 2019). We considered individual variables to be informative if the 85% confidence intervals did not overlap with 0 (Arnold 2010). Among the supported models we tested for differences in the model and the observed data using the Hosmer-Lemeshow goodness of fit test (Hosmer et al. 2013).

Results

A total of 499 adult white-tailed deer ($n_{\text{male}} = 343$, $n_{\text{female}} = 156$) were radio collared and monitored for mortality from 2011-2014 ($n_{2011} = 105$, $n_{2012} = 118$, $n_{2013} = 161$, $n_{2014} = 190$). The number of deer monitored was greater than the number of uniquely radio collared animals because some were monitored for >1 year. Mortality investigations confirmed 63 white-tailed deer kill sites where cause-specific mortality was classified as a canid ($n_{\text{wolf}} = 28$, $n_{\text{coyote}} = 35$). Among the 63 canid kill sites, 25% (16) were classified with uncertainty as being either wolf or coyote (Walsh et al. 2018). 79% (50) of the kills occurred between 1 January and 30 April ($n_{\text{wolf}} = 19$, $n_{\text{coyote}} = 31$). The number of mortalities ($n_{2011} = 7$, $n_{2012} = 8$, $n_{2013} = 18$, $n_{2014} = 30$) showed significant variation among years ($\chi^2 = 8.63$, $df = 3$, $p = 0.03$).

Under the UU design the top model was the 'Snow depth' model ($\Delta AIC = 0.00$, $wAIC = 0.68$; Table 3a). Within the 'Snow depth' model the parameter indicated that the probability of a

kill site increased as snow depth increased ($\hat{\beta}_{\text{SNWD}} = 0.52$, 85% CI = 0.35 to 0.69; Figure 2a). Goodness of fit for the ‘Snow depth’ model indicated no difference between the model and the observed data ($\chi^2 = 10.09$, $df = 8$, $p = 0.26$). Biologically relevant models included ‘Snow depth and cover’ model ($\Delta\text{AIC} = 2.92$, $w\text{AIC} = 0.16$; Table 3a), and ‘Snow depth and roads’ model ($\Delta\text{AIC} = 2.98$, $w\text{AIC} = 0.15$; Table 3a). Within the ‘Snow depth and cover’ model, the parameter for snow depth showed a positive effect ($\hat{\beta}_{\text{SNWD}} = 0.53$, 85% CI = 0.36 to 0.70), while other parameters were uninformative ($\hat{\beta}_{\text{CONF}} = 0.03$, 85% CI = -0.18 to 0.22; $\hat{\beta}_{\text{SNWD} \times \text{CONF}} = -0.53$, 85% CI = -0.29 to 0.05). Within the ‘Snow depth and roads’ model, the parameter for snow depth showed a significant positive effect ($\hat{\beta}_{\text{SNWD}} = 0.53$, 85% CI = 0.35 to 0.69), while other parameters were uninformative ($\hat{\beta}_{\text{RLEN}} = -0.06$, 85% CI = -0.29 to 0.14; $\hat{\beta}_{\text{SNWD} \times \text{RLEN}} = -0.07$, 85% CI = -0.23 to 0.09).

The top supported model for the UA design was the ‘Snow depth’ model ($\Delta\text{AIC} = 0.00$, $w\text{AIC} = 0.63$; Table 3b). The ‘Snow depth’ model indicated the probability of a kill increased as snow depth increased ($\hat{\beta}_{\text{SNWD}} = 0.64$, 85% CI = 0.47 to 0.80; Figure 2b). Goodness of fit for the ‘Snow depth’ model indicated no significant difference between the model and the observed data ($\chi^2 = 7.07$, $df = 8$, $p = 0.53$). Biologically relevant models included the ‘Global’ model ($\Delta\text{AIC} = 2.87$, $w\text{AIC} = 0.15$; Table 3b), the ‘Snow depth and roads’ model ($\Delta\text{AIC} = 3.42$, $w\text{AIC} = 0.11$; Table 3b), and the ‘Snow depth and cover’ model ($\Delta\text{AIC} = 3.58$, $w\text{AIC} = 0.11$; Table 3b). Parameters within the ‘Global’ model showed non-zero effects for snow depth and broad-leaved deciduous forest, with a positive effect for snow depth and a negative effect for broad-leaved deciduous forest ($\hat{\beta}_{\text{SNWD}} = 0.65$, 85% CI = 0.48 to 0.82; $\hat{\beta}_{\text{BLDF}} = -0.62$, 95% CI = -0.89 to -0.34). Parameters within the ‘Snow depth and roads’ model indicated a significant effect for snow depth, where the probability of a kill increased as snow depth increased ($\hat{\beta}_{\text{SNWD}} = 0.64$, 85% CI =

0.48 to 0.80), while other parameters were uninformative ($\hat{\beta}_{\text{RLEN}} = -0.12$, 85% CI = -0.37 to 0.11; $\hat{\beta}_{\text{SNWD} \times \text{RLEN}} = -0.01$, 85% CI = -0.17 to 0.19). Within the 'Snow depth and cover' model, the parameter for snow depth showed a positive effect ($\hat{\beta}_{\text{SNWD}} = 0.64$, 85% CI = 0.48 to 0.81), while other parameters were uninformative ($\hat{\beta}_{\text{CONF}} = 0.05$, 85% CI = -0.18 to 0.25; $\hat{\beta}_{\text{SNWD} \times \text{CONF}} = -0.04$, 85% CI = -0.12 to 0.20).

Discussion

Our results indicate white-tailed deer mortality risk from wolf and coyote predation increases as snow depth increases. This finding is consistent with existing research linking white-tailed deer predation rates to increases in snow depth (Nelson and Mech 1986; DelGiudice et al. 2002; Vucetich 2012). The instantaneous effect of snow depth on deer predation has been linked to the physical properties of snow influencing deer mobility. For example, white-tailed deer have higher foot loading than canids, reducing their ability to escape predation in deep snow (Nelson and Mech 1986; Vucetich et al. 2012). Our results reflect the effects of snow depth on predation risk within a relatively short temporal window, therefore we could not isolate the relative effects of snow depth on physical mobility from the more gradual effect of snow duration on deer energetics and body condition. For example, deteriorating body condition throughout the winter may be a primary cause of increased vulnerability to predation (DelGiudice et al. 2002; DelGiudice et al. 2013; Kautz et al. 2020). Decoupling the effects of snow depth and duration relative to predation risk will require fine-scale metrics on the physical properties of snow depth, duration, and deer body condition (Penczykowski et al. 2017). Understanding this relationship may elucidate fine scale indicators of population productivity such as birth rate and population growth (DeCesare et al. 2014).

We did not find an indication that spatially explicit landscape features such as vegetation, agriculture, water, human activity, or roads influenced spatial patterns of kill sites. This result is reasonable in our study system considering there were relatively low amounts of spatial heterogeneity in terms of land cover or disturbance that are key components of predation risk in other predator-prey systems (Kunkel and Pletscher 2000; Hebblewhite et al. 2005a; Kauffman et al. 2007). Additionally, our study system lacked topographical complexity, which has been shown to have a strong influence on spatial patterns of ungulate predation risk (Kittle et al. 2008; Torretta et al. 2018).

We found that coyotes were a substantial source of predation on adult white-tailed deer during our study, despite the risk of living among sympatric wolves (Switalski 2013). This finding could be due to niche partitioning of non-limiting food resources (Paquet 1992). We note, however, that there was some uncertainty in classification of cause-specific mortality between wolves and coyotes. For example, 25% of our kill sites were classified with some weight to cause of death being either wolf or coyote (Walsh et al. 2018). This complicated our ability to understand environmental differences and niche partitioning between wolf and coyote predation. Our results and other recent research (Kautz et al. 2020) suggest the need for an expanded focus on the influence of coyote predation on adult white-tailed deer.

Snow cover is expected to decline in the northern hemisphere, especially earlier in the spring (Choi et al. 2010) and changing snow pack may affect the outcomes of ecological interactions such as decreasing consumption of ungulates by apex predators (Nelson and Mech 1986; Penczykowski et al. 2017). In Minnesota, wolves changed their feeding behavior in response to snow-induced changes in white-tailed deer distribution and mobility such as spending less time with other pack members and traveling farther and more often (Fuller 1991).

Because predation patterns change with prey abundance during mild winters predator populations may seek alternative food sources (Johansson et al. 2015). The effect and consequences of global climate change on white-tailed deer, community, and trophic interactions will require a better understanding of snow dynamics on this predator-prey system.

The behaviors of predator hunting and prey defense have unique spatial components occurring at multiple spatial scales (Hebblewhite et al. 2005a). Predatory avoidance strategies of white-tailed deer may depend on situation-specific defense decisions, and available escape features (Mech and Peterson 2003). Some ungulates such as wild sheep and goats outmaneuver wolves using steep and dangerous terrain (Mech and Peterson 2003), while others such as white-tailed deer, moose (*Alces alces* (Linneus, 1758)), and caribou may associate with shorelines during the summer, escaping to open water as an antipredator strategy (Nelson and Mech 1981; Stephens and Peterson 1984; Bergerud 1985). We examined predation at a relatively large spatial scale at which the encounter, attack, and kill may occur, potentially limiting our inference to broad-scale predictors of relative mortality risk. We had a limited ability to infer fine-scale canid behavior and space use without locations of individuals. We used estimated wolf pack territories, but these were limited in terms of constructing a species utilization distribution (Kauffman et al. 2007). Combining location information from both collared predators and prey at fine-scale sampling intervals has allowed researchers to directly assess behavioral space use patterns and should be considered for future studies (Hebblewhite et al. 2005a; Hebblewhite and Merrill 2009; DeCesare et al. 2014).

Understanding the effect of snow on white-tailed deer populations is critical for population management, however, snow depth and snow cover duration is difficult to predict or manipulate. Thus, wildlife managers are limited in terms of proactive strategies for managing the

impacts of predation on white-tailed deer populations. Despite less snow cover expected in the northern hemisphere, heterogeneity in winter severity and snow cover within regions is common (Choi et al. 2010). White-tailed deer in the northern extent of their range have the propensity to migrate between summer and winter range to access seasonal food sources and reduce risk of predation (Van Deelen et al. 1998). Managers should consider this evolutionary strategy when considering forest management decisions that impact dynamic use of winter and summer deer range and the potential for migration between them. While the majority of research on migratory movements of ungulates has taken place in the western United States (Fryxell et al. 1988; Hebblewhite and Merrill 2009; Merkle et al. 2016; Sawyer et al. 2016; Aikens et al. 2017) the importance of migratory movement among white-tailed deer has received little attention but may give insights to differential survival and long-term herd health, as well as the capacity for white-tailed deer to minimize the impacts of canid predation (Hoskinson and Mech 1976; Van Deelen et al. 1998; Brinkman et al. 2009).

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References

- Aikens, E.O., Kauffman, M.J., Merkle, J.A., Dwinell, S.P.H., Fralick, G.L., and Monteith, K.L. 2017. The greenscape shapes surfing of resource waves in a large migratory herbivore. *Ecology Letters* **20**(6): 741-750. doi:10.1111/ele.12772.
- Allen, M.L., Elbroch, L.M., Casady, D.S., and Wittmer, H.U. 2014. Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Canadian Journal of Zoology* **92**: 397-403. doi:10.1139/cjz-2013-0284.
- Allen, M.L., Harris, R.E., Olson, L.O., Olson, E.R., Van Stappen, J., and Van Deelen, T.R. 2019. Resource limitations and competitive interactions affect carnivore community composition at different ecological scales in a temperate island system. *Mammalia* **83**(6): 552-561. doi:doi:10.1515/mammalia-2017-0162.
- Alverson, W.S., Waller, D.M., and Solheim, S.L. 1988. Forests too deer: Edge effects in northern Wisconsin [https://doi.org/10.1111/j.1523-1739.1988.tb00199.x]. *Conservation Biology* **2**(4): 348-358. doi:https://doi.org/10.1111/j.1523-1739.1988.tb00199.x.
- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* **74**(6): 1175-1178. doi:10.2193/2009-367.
- Barber-Meyer, S.M., Mech, L.D., Newton, W.E., and Borg, B.L. 2016. Differential wolf-pack-size persistence and the role of risk when hunting dangerous prey. *Behaviour* **153**: 1473-1487. doi:10.1163/1568539X-00003391.
- Barrett, M.W., Nolan, J.W., and Laurence, D.R. 1982. Evaluation of a hand-held net-gun to capture large mammals. *Wildlife Society Bulletin* **10**: 108-114. Available from <https://www.jstor.org/stable/pdf/3781727.pdf>.

- Bartón, K. 2016. MuMIN: multi-model inference. R package. Available from <http://CRAN.R-project.org/package=Mumin>.
- Berger, J. 2007. Fear, human shields and the redistribution of prey and predators in protected areas. *Biology Letters* **3**: 620-623. doi:10.1098/rsbl.2007.0415.
- Bergerud, A.T. 1985. Antipredator strategies of caribou: dispersion along shorelines. *Canadian Journal of Zoology* **63**: 1324-1329. Available from www.nrcresearchpress.com.
- Beyer, H.L. 2009. Geospatial modelling environment. Available from <http://www.spatialecology.com/gme>.
- Boyce, M.S., and McDonald, L.L. 1999. Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* **14**: 268-272. doi:10.1016/0363-5023(94)90184-8.
- Boyce, M.S., Vernier, P.R., Nielsen, S.E., and Schmiegelow, F.K.A. 2002. Evaluating resource selection functions. *Ecological Modelling* **157**: 281-300. doi:10.1016/S0304-3800(02)00200-4.
- Breton, L., and Potvin, F. 1988. Use of a net gun for capturing white-tailed deer *Odocoileus virginianus* on Anticosti Island, Quebec. *Canadian Field Naturalist* **102**: 697-700.
- Burnham, K.P., and Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Brinkman, T., DePerno, C., Jenks, J., Haroldson, B., and Osborn, R. 2009. Movement of female white-tailed deer: Effects of climate and intensive row-crop agriculture. *Journal of Wildlife Management* **69**: 1099-1111. doi:10.2193/0022-541X(2005)069[1099:MOFWDE]2.0.CO;2.

- Choi, G., Robinson, D.A., and Kang, S. 2010. Changing northern hemisphere snow seasons. *Journal of Climate* **23**: 5305-5310. doi:10.1175/2010JCLI3644.1.
- Clover, M.R. 1956. Single-gate deer trap. *California Fish and Game* **42**: 199-201.
- Creel, S., Winnie, J.A., and Christianson, D. 2013. Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution* **3**: 5189-5200. doi:10.1002/ece3.896.
- Curtis, J.T. 1959. *Vegetation of Wisconsin*. The University of Wisconsin Press, Madison, WI.
- de Boer, W.F., Vis, M.J.P., de Knegt, H.J., Rowles, C., Kohi, E.M., van Langevelde, F., et al. 2010. Spatial distribution of lion kills determined by the water dependency of prey species. *Journal of Mammalogy* **91**: 1280-1286. doi:10.1644/09-MAMM-A-392.1.
- DeCesare, N.J., Hebblewhite, M., Bradley, M., Hervieux, D., Neufeld, L., and Musiani, M. 2014. Linking habitat selection and predation risk to spatial variation in survival. *Journal of Animal Ecology* **83**(2): 343-352. doi:10.1111/1365-2656.12144.
- Delgiudice, G.D., Sampson, B.A., and Giudice, J.H. 2013. A long-term assessment of the effect of winter severity on the food habits of white-tailed deer. *Journal of Wildlife Management* **77**(8): 1664-1675. doi:10.1002/jwmg.616.
- DelGiudice, G.D., Riggs, M.R., Joly, P., and Pan, W. 2002. Winter severity, survival, and cause-specific mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife Management* **66**(3): 698-717. Available from <https://www.jstor.org/stable/pdf/3803136.pdf>.
- Dickie, M., Serrouya, R., McNay, R.S., and Boutin, S. 2017. Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology* **54**(1): 253-263. doi:10.1111/1365-2664.12732.

- Esri. 2014. ArcGIS Desktop. Environmental Systems Research Institute, Redlands, CA.
- Esri. Topographic Basemap. Scale Not Given. World Topographic Map. January 13, 2020.
Available from <https://www.arcgis.com/home/item.html?id=a1dc28de08e6447c8d14085fa15012e1>.
- Ferguson, S.H., Bergerud, A.T., and Ferguson, R. 1988. Predation risk and habitat selection in the persistence of a remnant caribou population. *Oecologia* **76**: 236-245. Available from <https://link.springer.com/content/pdf/10.1007/BF00379957.pdf>.
- Fryxell, J.M., Greever, J., and Sinclair, A.R.E. 1988. Why are migratory ungulates so abundant? *The American Naturalist* **131**: 781-798. Available from <https://www.jstor.org/stable/pdf/2461813.pdf?refreqid=excelsior%3A59ac74a95139e0190e94b8fa9504d659>.
- Fuller, T.K. 1991. Effect of snow depth on wolf activity and prey selection in north central Minnesota. *Canadian Journal of Zoology* **69**(3): 821-821. doi:10.1139/z91-123.
- Gilbert, S.L., Hundertmark, K.J., Person, D.K., Lindberg, M.S., and Boyce, M.S. 2017. Behavioral plasticity in a variable environment: snow depth and habitat interactions drive deer movement in winter. *Journal of Mammalogy* **98**(1): 246-259. doi:10.1093/jmammal/gyw167.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, et al. 2006. Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* **75**(4): 887-898. doi:10.1111/j.1365-2656.2006.01106.x.
- Halls, L.K. 1984. White-tailed Deer Ecology and Management. Stackpole Books, Harrisburg.

- Hebblewhite, M. 2005. Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. *Journal of Animal Ecology* **74**(2): 226-233. doi:10.1111/j.1365-2656.2004.00909.x.
- Hebblewhite, M., and Merrill, E.H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* **90**(12): 3445-3454. doi:10.1890/08-2090.1.
- Hebblewhite, M., Merrill, E.H., and McDonald, T.L. 2005*a*. Spatial decomposition of predation risk using resource selection functions: an example in a wolf-elk predator prey system. *Oikos* **111**: 101-111. doi:10.1111/j.0030-1299.2005.13858.x.
- Hebblewhite, M., White, C.a., Nietvelt, C.G., McKenzie, J.a., Hurd, T.E., Fryxell, J.M., Bayley, S.E., and Paquet, P.C. 2005*b*. Human activity mediates a trophic cascade caused by wolves. *Ecology* **86**(8): 2135-2144. Available from http://scholarworks.umt.edu/biosci_pubs/288.
- Hoskinson, R.L., and Mech, L.D. 1976. White-tailed deer migration and its role in wolf predation. *Journal of Wildlife Management* **40**(3): 429-441.
- Hosmer Jr, D.W., Lemeshow, S., and Sturdivant, R.X. 2013. Applied logistic regression. 3rd ed. John Wiley & Sons, Hoboken, NJ.
- Johansson, Ö., McCarthy, T., Samelius, G., Andrén, H., Tumursukh, L., and Mishra, C. 2015. Snow leopard predation in a livestock dominated landscape in Mongolia. *Biological Conservation* **184**: 251-258. doi:10.1016/j.biocon.2015.02.003.

- Kauffman, M.J., Varley, N., Smith, D.W., Stahler, D.R., MacNulty, D.R., and Boyce, M.S. 2007. Landscape heterogeneity shapes predation in a newly restored predator-prey system. *Ecology Letters* **10**(8): 690-700. doi:10.1111/j.1461-0248.2007.01059.x.
- Kautz, T.M., Belant, J.L., Beyer Jr, D.E., Strickland, B.K., and Duquette, J.F. 2020. Influence of body mass and environmental conditions on winter mortality risk of a northern ungulate: Evidence for a late-winter survival bottleneck. *Ecology and Evolution* **10**(3): 1666-1677. doi:https://doi.org/10.1002/ece3.6026.
- Keating, K.A., and Cherry, S. 2004. Use and interpretation of logistic regression in habitat-selection studies. *The Journal of Wildlife Management* **68**(4): 774-789. doi:10.2193/0022-541X(2004)068[0774:UAIOLR]2.0.CO;2.
- Kittle, A.M., Fryxell, J.M., Desy, G.E., and Hamr, J. 2008. The scale-dependent impact of wolf predation risk on resource selection by three sympatric ungulates. *Oecologia* **157**(1): 163-175. doi:10.1007/s00442-008-1051-9.
- Kolenosky, G.B. 1972. Wolf predation on wintering deer in east-central ontario. *The Journal of Wildlife Management* **36**(2): 357-369. doi:10.2307/3799065.
- Kunkel, K.E., and Pletscher, D.H. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology* **78**(1): 150-157. doi:10.1139/z99-181.
- Lima, M., Stenseth, N.C., and Jaksic, F.M. 2002. Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects. *Proceedings of the Royal Society B* **269**: 2579-2586. doi:10.1098/rspb.2002.2142.

- Lima, S.L., and Dill, L.M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* **68**(4): 619-640. doi:10.1139/z90-092.
- Manly, B.F.J., McDonald, L.L., Thomas, D.L., McDonald, T.L., and Erickson, W.P. 2002. *Resource Selection by Animals*. Kluwer Academic Publishers.
- Mech, L.D. 1977. Wolf-pack buffer zones as prey reservoirs. *Science* **198**(4314): 320-321. doi:10.1126/science.198.4314.320.
- Mech, L.D., and Peterson, R.O. 2003. *Wolf-Prey Relations*. Edited by L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 131-160.
- Mech, L.D., and Boitani, L. 2003. *Wolf Social Ecology*. Edited by L.D. Mech and L. Boitani. The University of Chicago Press, Chicago. pp. 1-34.
- Mech, L.D., Harper, E.K., Meier, T.J., and Paul, W.J. 2000. Assessing factors that may predispose Minnesota farms to wolf depredations on cattle. *Wildlife Society Bulletin* **28**(3): 623-629. doi:10.2307/3783612.
- Merkle, J.A., Monteith, K.L., Aikens, E.O., Hayes, M.M., Hersey, K.R., Middleton, A.D., et al. 2016. Large herbivores surf waves of green-up during spring. *Proceedings of the Royal Society B: Biological Sciences* **283**(1833). doi:10.1098/rspb.2016.0456.
- Mladenoff, D.J., Clayton, M.K., Pratt, S.D., Sickley, T.A., and Wydeven, A.P. 2009. Change in occupied wolf habitat in the Northern Great Lakes Region. Edited by A.P. Wydeven and T.R. Van Deelen and E.J. Heske. Springer Science+Business Media, LLC, New York. pp. 119-138.
- Muhly, T.B., Semeniuk, C., Massolo, A., Hickman, L., and Musiani, M. 2011. Human activity helps prey win the predator-prey space race. *PLoS ONE* **6**(3): e17050-e17050. doi:10.1371/journal.pone.0017050.

- Nelson, M.E., and Mech, L.D. 1981. Deer social organization and wolf predation in northeastern Minnesota. *Wildlife Monographs* **77**: 3-53. Available from <https://www.jstor.org/stable/pdf/3830578.pdf>.
- Nelson, M.E., and Mech, L.D. 1986. Relationship between snow depth and gray wolf predation on white-tailed deer. *The Journal of Wildlife Management* **50**(3): 471-474. Available from <http://www.jstor.org/stable/3801108>.
- Nelson, M.E., and Mech, L.D. 1986. Mortality of white-tailed deer in northeastern Minnesota. Source: *The Journal of Wildlife Management* **50**(4): 691-698. Available from <http://www.jstor.org/stable/3800983> <http://about.jstor.org/terms>.
- Newton, E.J., Patterson, B.R., Anderson, M.L., Rodgers, A.R., Vander Vennen, L.M., and Fryxell, J.M. 2017. Compensatory selection for roads over natural linear features by wolves in northern Ontario: Implications for caribou conservation. *PLoS ONE* **12**(11): e0186525-e0186525. doi:10.1371/journal.pone.0186525.
- Norton, A.S. 2015. Integration of harvest and time-to-event data used to estimate demographic parameters for white-tailed deer. Ph.D. dissertation, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison.
- Ozoga, J.J. 1968. Variations in microclimate in a conifer swamp deeryard in northern Michigan. *The Journal of Wildlife Management* **32**: 574-585. Available from <https://www.jstor.org/stable/pdf/3798938.pdf?refreqid=excelsior%3Aa2682f56f71905c3e729d5214750c830>.
- Ozoga, J.J., and Harger, E.M. 1966. Winter activities and feeding habits of northern Michigan coyotes. *The Journal of Wildlife Management* **30**(4): 809-818. doi:10.2307/3798288.

- Paquet, P.C. 1992. Prey use strategies of sympatric wolves and coyotes in Riding Mountain National Park, Manitoba. *Journal of Mammalogy* **73**(2): 337-343. doi:10.2307/1382067.
- Penczykowski, R.M., Connolly, B.M., and Barton, B.T. 2017. Winter is changing: Trophic interactions under altered snow regimes. *Food Webs* **13**: 80-91. doi:10.1016/j.fooweb.2017.02.006.
- R Core Team. 2018. R: A language and environment for statistical computing. Vienna, Austria.
- Ramsey, C.W. 1968. A drop-net deer trap. *The Journal of Wildlife Management* **32**: 187-190. Available from <https://www.jstor.org/stable/pdf/3798257.pdf>.
- Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., et al. 2014. Status and ecological effects of the world's largest carnivores. *Science* (New York, N.Y.) **343**(6167): 1241484-1241484. doi:10.1126/science.1241484.
- Rongstad, O.J., and McCabe, R.A. 1984. Capture techniques. *Edited by L.K. Halls*. Stackpole Books, Harrisburg, PA, USA. pp. 655-676.
- Rooney, T.P., McCormick, R.J., Solheim, S.L., and Waller, D.M. 2000. Regional variation in recruitment of hemlock seedlings and saplings in the Upper Great Lakes, USA. *Ecological Applications* **10**: 1119-1132. Available from <https://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1890/1051-0761%282000%29010%5B1119%3ARVIROH%5D2.0.CO%3B2>.
- Sawyer, H., Middleton, A.D., Hayes, M.M., Kauffman, M.J., and Monteith, K.L. 2016. The extra mile: Ungulate migration distance alters the use of seasonal range and exposure to anthropogenic risk. *Ecosphere* **7**(10): 1-11. doi:10.1002/ecs2.1534.
- Severinghaus, C.W. 1949. Tooth development and wear as criteria of age in white-tailed deer. *The Journal of Wildlife Management* **13**(2): 195-216.

- Sih, A. 2005. Predator-prey space use as an emergent outcome of a behavioral response race. *Edited by P. Barbosa and I. Castellanos*. Oxford University Press, Oxford, New York. pp. 394-394.
- Stephens, P.W., and Peterson, R.O. 1984. Wolf-avoidance strategies of moose. *Holarctic Ecology* **7**: 239-244. Available from <https://about.jstor.org/terms>.
- Stewart, K.M., Bowyer, R.T., and Weisberg, P.J. 2011. Spatial use of landscapes. *In* Biology and management of white-tailed deer. CRC Press, Boca Raton, FL. pp. 181-217.
- Switalski, T.A. 2003. Coyote foraging ecology and vigilance in response to gray wolf reintroduction in Yellowstone National Park. *Canadian Journal of Zoology* **81**(6): 985-993. doi:10.1139/z03-080.
- TIGER/Line Shapefiles. 2010. U. S. Census Bureau, Washington, D.C. Available from <https://www.census.gov/geographies/mapping-files/time-series/geo/tiger-line-file.html>.
- Torretta, E., Caviglia, L., Serafini, M., and Meriggi, A. 2018. Wolf predation on wild ungulates: how slope and habitat cover influence the localization of kill sites. *Current Zoology* **64**(3): 271-275. doi:10.1093/cz/zox031.
- Underwood, R. 1982. Vigilance behaviour in grazing African antelopes. *Behaviour* **79**(2-4): 81-107. doi:10.1163/156853982X00193.
- Van Deelen, T.R., Campa, H., Hamady, M., and Haufler, J.B. 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in northern Michigan. *The Journal of Wildlife Management* **62**: 205-205. doi:10.2307/3802280.
- Vucetich, J.A., Huntzinger, B.A., Peterson, R.O., Vucetich, L.M., Hammill, J.H., and Beyer Jr, D.E. 2012. Intra-seasonal variation in wolf *Canis lupus* kill rates. *Wildlife Biology* **18**(3): 235-245. doi:10.2981/11-061.

- Walsh, D.P., Norton, A.S., Storm, D.J., Van Deelen, T.R., and Heisey, D.M. 2018. Using expert knowledge to incorporate uncertainty in cause-of-death assignments for modeling of cause-specific mortality [<https://doi.org/10.1002/ece3.3701>]. *Ecology and Evolution* **8**(1): 509-520. doi:<https://doi.org/10.1002/ece3.3701>.
- Wang, Y., Allen, M.L., and Wilmers, C.C. 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. *Biological Conservation* **190**: 23-33. doi:10.1016/j.biocon.2015.05.007.
- Warbington, C.H., Van Deelen, T.R., Norton, A.S., Stenglein, J.L., Storm, D.J., and Martin, K.J. 2017. Cause-specific neonatal mortality of white-tailed deer in Wisconsin, USA. *Journal of Wildlife Management* **81**(5): 824-833. doi:10.1002/jwmg.21260.
- Wilmers, C.C., Wang, Y., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., et al. 2013. Scale dependent behavioral responses to human development by a large predator, the puma. *PLoS ONE* **8**(4). doi:10.1371/journal.pone.0060590.
- Wisconsin Department of Natural Resources. 2016. Wiscland 2.0 User Guide. Madison, WI, USA.
- Wisconsin Department of Natural Resources. 2010. Wisconsin State Boundary 24K. Madison, WI, USA. Available from <https://data-wi-dnr.opendata.arcgis.com/datasets/wisconsin-state-boundary-24k?geometry=-106.412%2C42.003%2C-73.035%2C47.460>.
- Wydeven, A.P., Wiedenhoeft, J.E., Schultz, R.N., Thiel, R.P., Jurewicz, R.L., Kohn, B.E., and Van Deelen, T.R. 2009. History, Population Growth, and Management of Wolves in Wisconsin. *Edited by* A.P. Wydeven and T.R. Van Deelen and E.J. Heske. Springer Science+Business Media, LLC, New York. pp. 87-105.

Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., and Liberg, O. 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. *Behav Ecol* 25:1353-1364. doi:10.1093/beheco/aru134.

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Table 1. Individual variables and expected effect considered in *a-priori* models of white-tailed deer (*Odocoileus virginianus*) predation risk by wolves (*Canis lupus*) and coyotes (*Canis latrans*) in northern Wisconsin, USA, from 2011-2014. Numbers in parenthesis indicate Wiscland 2.0 land cover classification codes.

Variable Name	Symbol	Unit	Effect	Description
Distance to wolf pack territory center	DWPC	m	+	Linear distance to center of nearest wolf pack territory center.
Developed	DVLP	%	+	Proportion of human activity and land use within kill site (1100, 1200).
Agriculture	AGRI	%	+	Proportion of agriculture row crop production or pasture used for livestock forage within kill site (2110, 2120, 2130, 2140, 3120).
Coniferous forest	CONF	%	+	Proportion of closed canopy where >67% is coniferous tree group or >50% swamp conifers within kill site (4110, 4120, 4130, 6410).
Broad leaf deciduous/mixed forest	BLDF	%	+	Proportion of closed canopy where >67% is broad-leaved deciduous tree group (4210, 4220, 4230, 4240, 4250) or mixed deciduous/coniferous tree group within kill site.
Open water	WATR	%	+	Proportion of water with no vegetation within kill site (5000).
Roads	RLEN	m	-	Linear amount of roads within kill site (TIGER line classification codes S1400, S1500, S1640, S1710, S1740, S1820).
Edge	EDGE	m	-	Linear amount of edge between land cover classifications from Wiscland 2.0 Level 1 within kill site.
Snow depth	SNWD	cm	-	Snow depth average from 7 days prior to day of deer carcass location from weather station in Winter, WI, USA.

Table 2. *A-priori* candidate models for white-tailed deer (*Odocoileus virginianus*) predation risk by wolves (*Canis lupus*) and coyotes (*Canis latrans*) in northern Wisconsin, USA, from 2011-2014.

Model Name	Variables	Support
Global	All	Predation risk is a complex process predicted by all variables.
Null	(.)	Predation risk is independent of spatial covariates.
Proximity to wolf pack	DWPC+(DWPC) ²	Wolves first kill white-tailed deer from the core of their territory then from the edges (Mech 1977) and wolf territories may be associated with coyote movement (Paquet 1992; Switalski 2003).
Human activity	DVLP+AGRI+RLEN	Humans alter habitat use by carnivores (Hebblewhite et al. 2005b; Wang et al. 2015), and may displace predators but not prey (Muhly et al. 2011).
Agriculture	AGRI+DVLP+AGRI x DVLP	Agriculture and human activity provides food and potentially refuge from predators (Muhly et al. 2011).
Water	WATR	Open bodies of water may be used as escape cover from predation (Bergerud 1985; Nelson and Mech 1981).
Cover	CONF	During the winter, coniferous cover provides thermal benefits and increased ability to avoid predators (Delgiudice et al. 2013; Nelson and Mech 1981; Ozoga 1968).
Forage	AGRI + BLDF	Agriculture and browse forage may affect the distribution of white-tailed deer and therefore kill sites (Kittle et al. 2008).
Snow	SNWD	Deep snow increases energy demands, lowering body condition of white-tailed deer over time and impeding escape from predators (DelGiudice et al. 2002; Nelson et al. 1986).
Snow depth and cover	SNWD+CONF+SNWD x CONF	Ungulates favor habitat with less snow provided by dense coniferous cover (Delgiudice et al. 2013; Fuller 1991; Nelson and Mech 1981; Penczykowski et al. 2017).
Snow depth and road density	SNWD+RLEN+SNWD x RLEN	Anthropogenic linear features may increase search efficiency and kill rate of canids, and the effect of roads may change in relationship to snow depth (Dickie et al. 2017; Newton et al. 2017).
Linear features	RLEN+EDGE	Anthropogenic linear features and edge may increase search efficiency and kill rate of canids (Berger 2007; Dickie et al. 2017; Newton et al. 2017).

Table 3a. Model selection results for UU white-tailed deer kill sites by wolves (*Canis lupus*) and coyotes (*Canis latrans*) in northern Wisconsin, USA, from 2011-2014.

Model Name	df	logLik	AIC	Δ AIC	w AIC
Snow depth	2	-213.57	431.14	0.00	0.68
Snow depth and cover	4	-213.03	434.07	2.92	0.16
Snow depth and roads	4	-213.06	434.13	2.98	0.15
Global	10	-209.49	438.98	7.84	0.01
Proximity to wolf pack	3	-220.38	446.77	15.62	0.00
Forage	3	-221.02	448.04	16.89	0.00
Water	2	-222.18	448.35	17.21	0.00
Null	1	-223.21	448.43	17.28	0.00
Cover	2	-223.21	450.42	19.28	0.00
Linear features	3	-222.78	451.56	20.42	0.00
Agriculture	4	-222.54	453.08	21.94	0.00
Human activity	4	-222.79	453.58	22.43	0.00

Table 3b. Model selection results for UA white-tailed deer kill sites by wolves (*Canis lupus*) and coyotes (*Canis latrans*) in northern Wisconsin, USA, from 2011-2014.

Model Name	df	logLik	AIC	ΔAIC	_w AIC
Snow depth	2	-195.78	395.57	0.00	0.63
Global	10	-189.22	398.44	2.87	0.15
Snow depth and roads	4	-195.49	398.98	3.42	0.11
Snow depth and cover	4	-195.57	399.15	3.58	0.11
Forage	3	-207.55	421.10	25.53	0.00
Null	1	-211.11	424.23	28.66	0.00
Agriculture	4	-208.60	425.21	29.64	0.00
Water	2	-211.01	426.02	30.45	0.00
Cover	2	-211.11	426.21	30.65	0.00
Linear features	3	-210.76	427.51	31.95	0.00
Human activity	4	-209.76	427.52	31.96	0.00
Proximity to wolf pack	3	-211.11	428.21	32.65	0.00

Figure 1. Map of the study area in Wisconsin, USA. This figure was created using ArcGIS Pro version 2.3.0 (Esri, Inc. 2018) and assembled from the following shapefiles: study area, kill site locations, and Wisconsin state boundary (WI DNR). The base map is from Esri World Topographic Base (Esri, DeLorme, NAVTEQ, TomTom, Intermap, increment P Corp, GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, Kadaster NL, Ordnance Survey, Esri Japan, METI, and the GIS User Community).

Figure 2. Predicted individual (UU, A) and population (UA, B) relative probability of mortality for white-tailed deer from wolves (*Canis lupus*) and coyotes (*Canis latrans*) (y-axis) and 95% confidence intervals around increasing snow depth (x-axis) in northern Wisconsin, USA.

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Figure 1. Map of the study area in Wisconsin, USA. This figure was created using ArcGIS Pro version 2.3.0 (Esri, Inc. 2018) and assembled from the following shapefiles: study area, kill site locations, and Wisconsin state boundary (WI DNR). The base map is from Esri World Topographic Base (Esri, DeLorme, NAVTEQ, TomTom, Intermap, increment P Corp, GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, Kadaster NL, Ordnance Survey, Esri Japan, METI, and the GIS User Community).

215x279mm (300 x 300 DPI)

Figure 2. Predicted individual (UU, A) and population (UA, B) relative probability of mortality for white-tailed deer from wolves (*Canis lupus*) and coyotes (*Canis latrans*) (y-axis) and 95% confidence intervals around increasing snow depth (x-axis) in northern Wisconsin, USA.

177x86mm (300 x 300 DPI)