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Factors Influencing White-Tailed Deer Mortality Risk within a Multi-Predator System in Michigan, USA

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Factors influencing white-tailed deer mortality risk within a multi-predator system in Michigan, USA.

By

Todd M. Kautz

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Factors influencing white-tailed deer mortality risk within a multi-predator system in Michigan, USA.

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I monitored cause-specific mortality and factors influencing mortality risk for white-tailed deer in the Upper Peninsula of Michigan, USA, during two high mortality risk periods: adult female deer during Feb–May, and fawns from birth to 6 months. I observed high rates of predation and starvation for adult female deer during Apr–May, suggesting that late winter represents a survival bottleneck due to nutritional declines. A strong negative relationship existed between snow free days during late winter and mortality risk. Predation was the dominant mortality source for fawns but predation risk decreased with larger birth mass. Black bears and coyotes accounted for most fawn kills at the population level, but wolves and bobcats had greatest per-individual fawn kill rates. My results suggest predation was the dominant mortality source for fawns and adult female deer, but multiple predator species were important and nutritional condition of deer influenced their vulnerability to predation.

DEDICATION

To Mom, for teaching me all I know about determination, hard work, dinosaurs, and vocabulary. To Matt, Jill, Tuck, and Jeff, for adventures in creeks, ponds, and hedgerows. To Dad, for his unfailing curiosity and support in his children’s interests, and for always stopping the tractor so that I could slide off the fender and move toads to safety.

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CHAPTER I

INTRODUCTION AND BASIS FOR RESEARCH

White-tailed deer (*Odocoileus virginianus*) are an important game species in Michigan and are also considered a keystone herbivore and have important impacts throughout their range by influencing the distribution, abundance, and ecosystem functions of other species (Paine 1969, Waller and Alverson 1997). In the mid-1990s, two consecutive severe winters in the Upper Peninsula of Michigan (UP) led to a decline in deer numbers, and the population has not since recovered. This sustained low abundance of deer in the UP has been correlated with evidence for concurrent increases in black bear (*Ursus americanus*), gray wolf (*Canis lupus*), and coyote (*Canis latrans*) abundance (MDNR, unpublished data). As these species are known to prey on white-tailed deer, it is important to understand their role in limiting deer abundance in the UP.

Additionally, winter temperature and snowfall varies considerably throughout the UP, with greater deer abundance generally associated with milder winter conditions (MDNR 2010). This suggests that white-tailed deer populations in the UP could be limited by winter weather (e.g. starvation during winter and spring; DePerno et al. 2002), or by factors influenced by winter weather (e.g. predation influenced by deer nutritional condition; Delguidice et al. 2000). Consequently, my goal was to evaluate survival and cause-specific mortality in adult and juvenile white-tailed deer in areas of the UP with low and moderate snowfall, and estimate how survival was influenced by weather and individual life history.

This research is part of an ongoing project titled “Role of predators, winter weather, and habitat on white-tailed deer fawn survival in the Upper Peninsula of Michigan”. Other research being conducted on the project includes measuring the dietary habits and abundance of black bear, gray wolf, coyote, and bobcat (*Lynx rufus*); as well as measuring the movements, resource selection, and annual abundance of white-tailed deer. Ultimately, this thesis will be combined with other results from this project to better understand the complex ecology of deer and predators in Michigan.

CHAPTER II

INFLUENCE OF BIOLOGICAL AND ENVIRONMENTAL CONDITIONS ON WINTER MORTALITY RISK OF A NORTHERN UNGULATE: EVIDENCE FOR A LATE-WINTER SURVIVAL BOTTLENECK.

Introduction

Identifying limiting factors for animals with seasonally dynamic life histories sometimes requires understanding intra-annual periods of resource scarcity (e.g., Ashmole 1963). For ungulates living in northern environments, winter is generally a period of negative energy budget when forage provides some energetic intake but most individuals rely heavily on fat stores accumulated during the previous summer and fall to survive until spring green-up (hereafter the nutritional integration model; Mautz 1979, Parker et al. 2009). Following this model, an annual survival bottleneck around the time of snowmelt could occur if the intensity and duration of winter are sufficient to exceed the energetic reserves of a substantial portion of the population (Parker et al. 2009).

An important prediction of the nutritional integration model is that the magnitude of late winter survival bottlenecks are influenced by multiple mechanisms: winter severity (usually measured by depth of snow and temperature) determines rate of energetic expenditure, duration of snow cover determines how long a negative energy budget persists, and body fat reserves carried into the winter from previous foraging seasons determine how much energy is available to lose before succumbing to mortality from starvation or other causes affecting weak animals (Parker et al. 2009). The importance of late winter survival for population dynamics of northern ungulates has been recognized (Clutton-Brock et al. 1991, Metz et al. 2012), yet determining which individual or environmental factors limit wild ungulate populations during late winter remains difficult due to the possible role of biological (e.g., nutritional status) and environmental (e.g., weather) conditions.

In most large ungulate species, adult female survival is typically higher, more stable, and less sensitive to environmental change than juvenile or adult male survival (McCullough 1979, Gaillard and Yoccoz 2003). In natural systems, female ungulates can have a life span exceeding 15 years (Loison et al. 1999), but generally succumb to one of numerous mortality agents (e.g., predation, starvation, disease, injury, exposure) before reaching their maximum potential longevity (Delguidice et al. 2006). The magnitude and timing of mortality for adult female free-ranging ungulates in temperate regions is influenced by habitat, predators, and weather with greatest non-hunting mortality often occurring during winter (Gaillard et al. 1998, Forrester and Wittmer 2012). Consequently, identifying which conditions result in high mortality risk for ungulates during winter is key to understanding what mechanisms are potentially limiting population growth.

For white-tailed deer (*Odocoileus virginianus* (Zimmerman, 1780)) populations near the northern edge of the species' range, late winter is a period of resource scarcity characterized by poor forage, low fat reserves, and highly concentrated deer densities within suitable winter habitat (Mautz 1978, DelGuidice et al. 2013, Nelson 1995, Dumont et al. 2005). Consequently, adult mortality from predation and malnutrition is generally greatest in northern deer populations during winter, particularly during Mar–Apr (Van Deelen et al. 1997, Whitlaw et al. 1998, DePerno et al. 2000, Dumont et al. 2000, DelGuidice et al. 2002).

The relationship between winter weather and survival of northern deer has led many natural resource agencies to adopt annual winter severity indexes (WSI) to predict deer population trends (Verme 1968, Leckenby and Adams 1986, Chadwick 2002, DelGuidice et al. 2002, Duquette et al. 2014b). These indexes attempt to relate one or more weather variables to deer population growth. Generally, snow depth and temperature have been considered important predictors of deer mortality, with wind sometimes playing an important role in more open habitats. Although ignoring the middle period of winter and considering only the early and late months of winter can result in a better index of weather effects on deer (Verme 1977), spring snowmelt date has not been considered as a predictor in adult deer survival models. Yet, spring snow depths appear to influence aspects of northern white-tailed deer ecology including migration behavior (Nelson 1995), habitat selection (Beier and McCullough 1990), and natal mortality (Verme 1977).

The Upper Peninsula of Michigan, USA, has a geographic gradient of snow conditions that is highly variable among years due to the climatic influence of the Great Lakes. Historically, deer population growth in the Upper Peninsula has been linked to variation in winter weather temporally and geographically (Leopold 1947, Doepker et al. 1996). The Upper Peninsula deer population declined due to consecutive severe winters in 1995–1996 and 1996–1997, but did not recover over the next 15 years while the recolonizing gray wolf (*Canis lupus* (L., 1758)) population increased during this same period (MDNR 2010, 2015).

Our goal was to use a mechanistic approach to test whether patterns of deer survival within late winter follows predictions from the nutritional integration model and determine which mechanisms most strongly influence survival. Cause-specific mortality of adult female white-tailed deer was investigated in relation to deer age, body mass, snow depth, cumulative WSI, and snowmelt timing in two areas with differing amounts of snowfall. We predicted that deer mortality risk would increase with greater snow depth, fewer snow free days during Feb–May, and decreasing body mass. These predictions were based on the hypothesis that deer generally maintain a negative energy balance during winter at northern latitudes, that weather conditions shape the rate of this nutritional decline, and that survival is dependent on conserving energetic stores until spring snow melt.

Study area

Data were collected from two study areas in the Upper Peninsula of Michigan, hereafter referred to as low-snowfall and mid-snowfall study areas. Both study areas contained populations of gray wolf, coyote (*Canis latrans* (Say, 1823)), and bobcat (*Lynx rufus* (Schreber, 1777)). The low-snowfall study area encompassed 319 km^2 in Menominee County (45°24'00" N 87°30'00" W; Fig. 1.1). Mean annual precipitation was 72.5 cm of rain and 128.8 cm of snow (1971–1996 averages, Michigan Climatology Office 2013a). Mean Jan and Jul temperatures were –8° C and 19° C, respectively (PRISM Climate Group 2016). Dominant land-covers included woody wetlands (52%), deciduous forest (14%), and agricultural (14%). The remaining 20% consisted of conifer forest, mixed forest, developed areas, herbaceous wetlands, shrub, and open water (Fry et al. 2011).

The mid-snowfall study area included 341 km^2 near the Michigamme Reservoir (46°14'00" N 88°13'00" W; Fig. 1.1) and was 65 km northwest of the low-snowfall study area. Mean annual precipitation was 52 cm of rain and 179 cm of snow (1951–1980 averages, Michigan Climatology Office 2013b). Mean Jan and Jul temperatures were –13° C and 18° C, respectively (PRISM Climate Group 2016). Land cover was predominantly deciduous forest (38%), woody wetland (29%), mixed forest (13%), and evergreen forest (6%) (Fry et al. 2011).

Methods

Deer capture and handling

Adult female white-tailed deer were captured during Feb–Apr 2009–2011 in the low snowfall study area and Feb–Mar 2013–2015 in the mid-snowfall study area. We captured deer primarily using Clover traps (Clover 1956) baited with shelled corn, alfalfa, and/or molasses, and occasionally used cannon nets. Deer were restrained, blindfolded, and immobilized with an intramuscular injection of ketamine hydrochloride (Putney, Inc., Portland, ME, USA) and xylazine hydrochloride (Lloyd Laboratories, Shenandoah, IA, USA) mixed at a 4:1 ratio and concentration of 100 mg/ml (Duquette et al. 2013). For each deer, body mass was recorded and age estimated by extracting a lower incisiform canine to age deer for counts of cementum annuli (Gilbert 1966, Nelson 2002) at the MDNR Diagnostic Center for Population and Animal Health (Lansing, MI, USA). Each deer was fitted with a VHF collar with an 8-hour movement mortality switch (Model M2510B; Advanced Telemetry Systems, Isanti, Minnesota, USA), and a vaginal implant transmitter with temperature switch and precise event transmitter to record time of temperature drop at half-hour intervals for up to 128 hours (Model M3930; Advanced Telemetry Systems, Isanti, Minnesota, USA). Before release, each deer received an intravenous or intramuscular injection of yohimbine hydrochloride (ZooPharm, Laramie, WY, USA) to reverse the effects of xylazine hydrochloride (Kreeger et al. 2002, Duquette et al. 2013). All animal handling procedures were approved by the Institutional Animal Care and Use Committee of Mississippi State University, Mississippi State, MS, USA.

Deer were monitored weekly using aerial- or ground-based telemetry. When a mortality signal was detected, the date and cause of mortality was determined based on deer remains and sign found at the mortality site. For predation events, evidence at the site (e.g., tracks, scat, canine puncture wounds, and site disturbance) was compared to published reports of predator-specific kills to estimate predator species (Cook et al. 1971, Mech et al. 1971, Nelson and Mech 1986). Mortalities were classified as unidentified predations if the mortality site showed evidence of predation (e.g., blood in surrounding snow, hemorrhaging on hide or tissue), but evidence was insufficient to assign a predator species or evidence of multiple predator species was present. Malnutrition status of mortalities was assessed using rump fat and bone marrow condition (Mech 2007) or by submitting carcasses for lab necropsy by a wildlife pathologist. In 68% of mortalities, investigations occurred <5.3 days after the time of mortality and date of mortality was determined to the nearest half hour using the precise event transmitter code of vaginal implant transmitters. For the remaining 32% of mortality events in which >5.3 days had passed, date of mortality was estimated using a combination of carcass decomposition, snow cover conditions, and telemetry records.

Weather data

The area of data collection for weather variables was determined by calculating the minimum convex polygon of mid-Mar aerial telemetry locations of deer, composite for all years within each study area. Ninety-two percent of deer telemetry locations collected during periods of snow cover between Nov and May occurred within these polygons. Daily snow depth estimates from 1 Nov to 31 May for each winter were obtained using 0.4-km resolution data from the National Snow and Ice Data Center Snow Data Assimilation System (National Operational Hydrologic Remote Sensing Center 2004) and averaged daily snow depth estimates within each study area. Daily minimum temperature values were obtained via remote sensing estimates from the PRISM climate group (2016) at the centroid of each study area. A daily winter severity index was calculated by first assigning each day one point if minimum temperature was $< -17.8^{\circ}$ C and one point if snow depth was >38.1 cm (DelGuidice et al. 2002). From this, a cumulative winter severity index was calculated by summing daily values for each winter beginning 1 Nov.

Snow free days were defined as days from 1 Feb to 31 May when mean snow depth was <7 cm, a depth at which deer move from winter to spring range (Beier and McCullough 1990). Because mass gains for white-tailed deer during spring are gradual (DelGuidice et al. 1992), the number of snow free days were summed into cumulative snow free days each year to reflect a possible lag effect in the relationship between deer mortality risk and spring snowmelt.

Survival analysis

Factors were assessed for influence on adult female deer weekly survival from 1 Feb to 31 May using Cox proportional hazards mixed effects models in the package coxme (Therneau 2015) for program R (R version 3.4.1, www.r-project.org, accessed 15 Mar 2018). Because deer captured using clover traps and rocket nets can experience capture myopathy-related mortality (Beringer *et al.* 1996), deer were not included in survival models until 2 weeks post-capture. As yearling deer captured in this study had different patterns in body mass and pregnancy rates than older deer (Duquette et al. 2012), survival analysis was limited to deer >2.5 years old.

Biological covariates of deer mortality risk included age (years) and body mass. Adult female survival was expected to follow a parabolic trend peaking at 5–6 years of age before declining (Delguidice et al. 2006) and so it was modeled as a quadratic term. Because deer body mass declined with capture date, slope estimates from linear regressions of adult female body mass by capture date for each year were used to standardize body mass to 1 Feb (Festa-Bianchet and Jorgenson 1998).

Time-specific covariates were included for cumulative winter severity index, cumulative snow-melt days, and snow depth, estimated for each week within years by averaging daily values over each weekly survival interval. Time-specific covariates can be incorporated into Cox proportional hazards models without confounding individual effects because the likelihood-estimation for a given interval is independent of other time intervals (Therneau et al. 2016). A staggered entry design was used to account for varying capture dates of deer (Pollock et al. 1989).

Low-snowfall or mid-snowfall study area were included as a random effect in all models to account for variation in predator populations, land-cover, and other factors which may influence deer mortality risk among study areas (Pankratz et al. 2005). Multi-collinearity among covariates was tested for using Spearman's rank correlation tests, and considered any covariates with $|r| < 0.7$ suitable for inclusion in the same model (Dormann et al. 2013). Although Cox proportional hazards models have fewer assumptions than parametric survival models, an important assumption is that the baseline hazard ratio for each covariate remains constant over time. Violations of this assumption were tested for by including a time interaction with each predictor covariate (Bellera et al. 2010), and in cases where the predictor covariates showed evidence of non-proportional hazards, the interaction term was included in final model selection to account for temporal change in hazard rate (Fox and Weisberg 2011). The final candidate model set included 24 candidate models with non-collinear covariate combinations of 6 factors: age, body mass, body mass:time interaction, weekly average snow depth, cumulative winter severity index, cumulative snow-free days. Because the goal was to explore the relative predictive value of model covariates on weekly deer survival, all candidate models were evaluated using backwards step-wise model ranking based on Akaike's Information Criterion adjusted for small samples, where candidate models <2 ΔAIC_c of the top-ranked model were considered competing models (Burnham and Anderson 2002, Symonds and Mouselli 2011). Statistical significance was established at $\alpha < 0.05$.

Results

One hundred fifty adult female deer (>2.5 years old) were captured, representing 1,784 deer-weeks of monitoring. Median date of capture was 10 Feb (interquartile range = 21 Jan–25 Feb). Estimated age of captured deer ranged from 2.5 to 16.5 years old (median = 6, interquartile range = 3–8). Annual mean body mass of captured adult female deer ranged from 54.3 to 64.0 kg, and mean body mass within the mid-snowfall study area (64.0 kg, SD = 5.8) was greater than the low-snowfall study area (57.9 kg, SD = 7.2; t(116) = 5.57, $P \leq 0.001$; Table 2.1). Pooled across all years, mean weekly mortality rate during Feb–May (2.1%) was 3.5 times greater than mean weekly mortality during Jun–Jan (0.6%).

Annual cumulative winter severity index values ranged from 11 to 167 (mean = 84.3, SD = 66.1) and annual cumulative snowmelt days ranged from 33 to 81 days (mean = 58, SD = 20; Table 2.1). Annual Feb–May survival estimates ranged from 0.24 to 0.89 (mean = 0.69, SD = 0.23). Weekly mortality rates were generally highest near the timing of snow-melt (Fig. 2.2). We observed 44 mortality events which we attributed to predation (*n* = 31), malnutrition (*n* = 8), drowning (*n* = 1), and unknown cause (*n* = 4; Table 2.2). Coyote (*n* = 12) and wolf (*n* = 11) were the most common predators of adult female deer, followed by unidentified predator (*n* = 6) and bobcat (*n* = 2). Of the 8 malnutrition mortalities, 6 occurred during the winter with greatest winter severity (2014; WSI = 167). No deer were censored due to radio collar failure or other reasons during the study interval.

Snow depth and cumulative snow free days were collinear (*r* = 0.92) and were not included in the same model. In the global model, body mass had a significant time-interaction (*P* = 0.028), so a body mass-time interaction was included in all candidate models to ensure that the proportional hazards assumption was not violated. After accounting for multi-collinear covariates and time interactions, we compared 24 candidate models. The best-supported model included body mass, body mass-time interaction, cumulative winter severity index, and cumulative snow free days; there were no competing models (Table 2.3). Mortality risk increased 1.7% with each unit increase of cumulative winter severity index (*P* = 0.003), decreased 7.2% with each cumulative snow free day (*P* = 0.002), and decreased 11.9% with each kg body mass greater than the population average (*P* = 0.011; Table 2.4). The interaction of time and body mass (*P* = 0.077) and age (*P* = 0.890) did not influence deer mortality risk at a significant level in the best-supported model. Scaled and centered covariate estimates of the top-ranked model suggested that deer survival was most sensitive to cumulative snow free days (coeff. = −1.72, SE = 0.55), with cumulative winter severity (coeff. = 0.91, SE = 0.30) and body mass (coeff. = −0.84, SE = 0.33) having similar predictive value.

Discussion

Influence of winter weather on mortality risk

The influence of winter weather on white-tailed deer winter survival is consistent with other studies of deer survival in northern climates (e.g., Nelson and Mech 1986, Dumont et al. 2000, DelGuidice et al. 2002). Our results indicated that the most critical period of winter deer survival is late winter-early spring (Apr and May) when snow melt occurs, but mortality risk varied widely depending on weather conditions. Our best-ranked model predicted that mortality risk was greatest immediately before snow spring snow melt, but mortality risk during this period varied considerably depending on weather conditions. For example, the maximum predicted mortality risk for a deer of average body mass varied from a 21-fold increase during 2014 (greatest winter severity) to a 1.2-fold increase in 2010 (least winter severity). Similarly, we observed a wide range of Feb–May adult female deer survival rates among years (Table 2.1), although the survival of 0.24 during 2014 was markedly lower than other winters. While our model predicted mortality risk to be greatest immediately before snow melt, observed mortality rates during 2013 and 2014, the two years with latest snow melt, remained high for 1-2 weeks following snow melt (Fig. 2.2). This could indicate a lag effect of snow conditions on deer mortality risk which our model did not account for. Such a lag effect may be expected because following snow melt deer physical condition is likely at an annual nadir and nutritional recovery from winter is a process which takes several weeks to begin (DelGuidice et al. 1992). Both our model estimates and observed patterns of mortality are consistent, however, in suggesting that after 3 weeks of snow free conditions, deer mortality risk is greatly reduced even following relatively severe winters.

A survival advantage for individuals with greater body mass has been noted in other ungulate populations with winter nutritional deficits (e.g., red deer (*Cervus elaphus*); Liosson et al. 1999). Increased seasonality in large homeothermic vertebrates is positively correlated with body mass, presumably because larger individuals are able to carry more energy reserves to endure longer periods of fasting (Lindstesdt and Boyce

1985, Boyce 1979). We believe that the positive relationship between survival and deer body mass, along with the larger average body mass of adult female deer within the mid-snowfall area, reflect a selective pressure for larger-bodied animals during prolonged winters. This provides further evidence that it is common for some northern ungulate populations to experience late winter and early spring conditions where nutritional margins for survival are thin.

The number of snow free days during Feb–May had an effect size on weekly mortality risk about twice as large as cumulative winter severity or body mass. Our best supported model estimated that deer mortality risk was reduced by 56% after 10 snow-free days, and 98% after 30 snow-free days. The number of snow free days in Feb–May is likely correlated to total winter severity index on an annual scale, but two winters can have similar WSIs with notable differences in spring snow melt. For example, winter 2012–2013 (winter severity index = 108; 33 snow-free days) had a lesser total winter severity index but 15 more days of snow cover during Feb–May than winter 2014-15 (winter severity index = 145; 48 snow-free days).

The greatest snow depths and coldest temperatures observed during this study occurred during Feb and early Mar, yet most deer mortality occurred during late Mar–early May. Additionally, weekly snow depth did not predict weekly deer survival. If the immediate physical effects of deep snow influenced deer mortality risk by impeding the ability to escape predators, snow depth would be positively correlated with deer mortality risk. In Minnesota, wolf predation rates on yearling and adult white-tailed deer were greatest during months with the deepest snow (Nelson and Mech 1986), and daily wolf kill rates of deer in a high snowfall area of Michigan were highly correlated to snow depth in a previous study (Vucetich et al. 2012). These studies suggest that the immediate effects of deep snow can increase predation on deer in some circumstances, but our results suggest that the gradual nutritional decline throughout winter was the primary mechanism influencing mortality risk during our study. A similar nutritional influence on white-tailed deer mortality was observed in South Dakota, where poor winter range conditions resulted in Apr–Jun adult female mortality rates exceeding 20% in 3 of 4 years (DePerno et al. 2000).

There are several possible explanations why deer mortality risk is strongly influenced by snow cover during late winter. First, pregnant female deer have a 45% increase in metabolic demands entering the third trimester of pregnancy (Pekins et al. 1998), which could result in a greater energy deficit for pregnant females during Apr and May even if dietary quality is similar during early winter. Likely as a result of pregnancy, declining forage, and cumulative energetic expenditure since the onset of winter, adult female northern deer are at an annual nutritional nadir during May (DelGuidice et al. 1992). Finally, crusted snow conditions during spring facilitate deer predation by wolves and coyotes because of heavier foot-loading in deer (Telfer and Kelsall 1984, Vucetich et al. 2012). With many deer in poor physical condition and snow conditions which favor predator movement, among-year differences of several weeks in the timing of spring snow melt could have a substantial effect on deer vulnerability to predation or malnutrition mortality.

A decrease in deer mortality risk following snow melt may be the result of several processes. First, deer foraging during deep snow conditions are limited to food available along established trails, where preferred browse species become depleted throughout winter (DelGuidice et al. 2013). Hobbs (1989) predicted that the energetic losses due to reduced forage intake and locomotion in deep snow were 5.4 times greater than losses due to increased thermoregulatory expenses in cold temperatures for mule deer (*O. hemonius*). Conditions of little or no snow depth facilitate movements and allow deer access to additional woody browse and ground forages. However, even with a positive energy budget, spring body mass gains by deer is a gradual process of weeks or months (DelGuidice et al. 1992). Consequently, deer may remain in relatively poor condition for several weeks following snow melt before making a nutritional recovery. In addition to nutritional gains, many deer in Michigan's Upper Peninsula undergo spring migration of up to 80 kilometers to traditional summer ranges shortly after snowmelt (Van Deelen et al. 1998). Possibly, the return of deer to more widely dispersed summer ranges from concentrated winter ranges could reduce predation risk by reducing predator encounter rates.

Cause-specific mortality and survival rates

Coyote and wolf predation were the leading mortality sources, accounting for 30% and 28%, respectively, of known cause mortalities. This is consistent with the general observation that where deer and large predators co-occur, predation tends to be the leading source of mortality (Ballard et al. 2001). Estimated coyote densities were 0.32–0.37 individuals/km^2 in the low snowfall study area and 0.19–0.24 individuals/km^2 in the mid snowfall study area (Petroelje et al. 2014, T. Petroelje unpublished data). Estimated wolf densities from winter track surveys were much lower, 0.012 individuals/km^2 in the low snowfall study area and 0.023–0.033 individuals/km^2 in the mid snowfall study area (MDNR, unpublished data). Thus, despite a similar number of adult female deer killed by coyotes and wolves, the number of deer killed per individual predator was probably much lower for coyotes and likely reflected greater densities of coyotes than wolves.

Elevated predation risk for prey with poor body condition has been commonly observed (e.g., Errington 1946, Murray 2002), and could result from both physical weakness in prey and increased foraging risks taken by starving individuals (predation-sensitive food hypothesis, Sinclair and Arcese 1995). Although our results suggest a link between deer nutritional condition and mortality risk, the greater question of additive vs. compensatory mortality from predators is beyond the scope of our study because it would require consideration of population growth rate and separate evaluation of mortality risk from predation and other causes.

The mean Feb–May survival of 0.69 in our study was notably low, considering that adult female annual survival in wild ungulates typically exceeds 0.80 (Gaillard and Yoccoz 2003). Low survival observed in our study was likely in part a consequence of severe winter conditions in the mid-snowfall study area, where the mean survival among 3 winters was 0.59. Observed survival within the low-snowfall area in our study was much greater (0.78), though lower than the estimated Jan–May survival of 0.89 for adult female deer in a low-snowfall area of the Upper Peninsula of Michigan during consecutive mild winters (Van Deelen et al. 1997). A possible source of additional mortality in our study was an increase in the estimated wolf population within the Upper Peninsula, from 80 to 637 individuals from 1995 to 2014 (MDNR 2015). However, the presence of wolves and severe winters does not always result in mortality rates as high as we observed. In Minnesota, USA, mean Nov–May survival of adult female deer sympatric with wolves, but not coyotes, was 0.91, with winter severity ranging from mild to historically severe (DelGuidice 2004). Though differences in habitat, predator density and composition, and deer density make direct comparison of winter mortality rates among studies difficult, low adult female winter survival in our study was a direct consequence of predation which we suggest was indirectly influenced by the effects of nutrition and weather.

Conclusions

We based our predictions on the hypothesis that deer generally maintain a negative energy balance during winter at northern latitudes, and survival is dependent on conserving energetic stores until spring snow melt. The positive relationship between cumulative winter severity index and mortality risk suggests that winters with deep snow and cold temperatures accelerate the decline of deer condition. The negative relationship between body mass and mortality risk suggests that larger deer are less susceptible to nutritional decline during late winter. Finally, the negative relationship between snow free days and mortality risk suggests that late-persisting deep snow conditions at the end of winter will strongly increase mortality risk, but risk will subside within 14–20 days after snow melt. Taken together, these conclusions suggest that deer in this population have a relatively low risk of mortality even under conditions of deep snow, as long as adequate nutritional reserves remain. However, once nutritional reserves are depleted, female deer of all age classes can experience high mortality rates from predation or starvation, especially during Apr–May, resulting in a survival bottleneck.

Evidence suggests that winter weather influences population dynamics of northern ungulates at annual and multi-year scales, likely though nutritional processes (Post and Stenseth 1998, Patterson and Power 2002), and our results suggest that similar interactions between nutrition and weather shape the short-term mortality risk of deer within winter and early spring. Overall, this supports the nutritional integration model of northern ungulate ecology suggested by Mautz (1979) and Parker et al. (2009). In future studies of northern ungulates with a negative energy budget during periods of snow cover, including snow free days during late winter or a similar measure of spring snowmelt timing in models may improve model accuracy and provide new insights into the timing, magnitude, and mechanisms of mortality.

Table 2.1 Summary of captured sample and survival covariates for radio-collared adult female white-tailed deer, Upper Peninsula of Michigan, USA, 1 Feb–31 May, 2009–2015.

Winter	Study area	N	Survival	Mean body mass (SE)[a]	Cumulative winter severity[b]	Cumulative snow free days[b]
2009	Low snowfall	25	0.89	54.3 (1.2)	60	74
2010	Low snowfall	20	0.72	59.7 (1.2)	11	81
2011	Low snowfall	18	0.74	57.6 (2.1)	15	74
2013	Mid snowfall	37	0.70	64.0 (0.9)	108	33
2014	Mid snowfall	27	0.24	63.6 (1.2)	167	38
2015	Mid snowfall	23	0.82	62.6 (1.4)	145	48

[a] Body mass adjusted to 1 Feb using regression by capture date.

[b] Cumulative values reflect values at the end of the monitoring period (31 May).

Table 2.2 Known fates of radio-collared adult female white-tailed deer, Upper Peninsula of Michigan, USA, 1 Feb–31 May, 2009–2015.

		Predation						
Winter	*n*	Bobcat	Coyote	Wolf	Unidentified	Malnutrition	Unknown	Survived
2009	25	0	2	0	0	0	0	23
2010	20	0	1	1	1	0	0	17
2011	18	1	0	1	0	1	1	14
2013	39	1	5	2	1	1	2	28
2014	27	0	4	4	3	6	2	7
2015	24	0	0	3	1	0	0	20
Total	150	2	12	11	6	8	4	106

Table 2.3 Model selection results using Akaike's Information Criterion adjusted for small sample sizes (AICc) for Cox-proportional hazards generalized linear mixed models estimating survival of radio-collared adult female white-tailed deer, Upper Peninsula of Michigan, USA, 1 Feb–31 May, 2009–2015. SFD represents cumulative snow free days, and WSI represents cumulative winter severity index. All models included study area as a random effect.

Covariate									
Age	Age^2	Mass	Snow depth	SFD[a]	WSI[b]	Mass:Time	df	ΔAIC_c	W_i
		-0.143		-0.083	0.018	0.010	4	0.00	0.122
-0.011	0.006	-0.155		-0.079	0.018	0.010	6	2.17	0.041
				-0.085	0.019		2	3.82	0.018
-0.173	0.015			-0.085	0.020		4	5.99	0.006
		-0.165		-0.061		0.012	3	7.86	0.002
0.095	-0.001	-0.180		-0.063		0.012	5	9.58	0.001
		-0.180			0.014	0.013	3	11.44	0
0.048	0.003	-0.198			0.016	0.014	5	12.02	0
		-0.171	-0.001		0.015	0.012	4	13.03	0
				-0.071			1	13.07	0
0.050	0.003	-0.189	-0.001		0.017	0.013	6	13.52	0
-0.100	0.010			-0.063			3	16.00	0
					0.014		1	17.18	0
			-0.001		0.015		2	18.20	0
-0.123	0.013				0.016		3	18.78	0
-0.105	0.012		-0.001		0.017		4	19.80	0
		-0.184				0.014	2	21.48	0
		-0.177	-0.001			0.013	3	22.65	0
0.157	-0.006	-0.209				0.015	4	22.82	0
0.151	-0.005	-0.201	-0.001			0.014	5	23.73	0
							0	27.77	0
			-0.001				1	28.46	0
-0.027	0.005						2	30.81	0
-0.022	0.005		-0.001				3	31.30	0

[a] Cumulative snow free days from 1 Nov to 31 May

[b] Cumulative winter severity index from 1 Nov to 31 May (DelGuidice et al. 2002).

Table 2.4 Estimates of scaled and centered covariates from the top-ranked Cox-proportional hazards generalized linear mixed model for weekly survival of radio-collared adult female white-tailed deer, Upper Peninsula of Michigan, USA, 2009–2015. Model included study area as a random effect.

Covariate	Coeff	SE	*Z*	*P*
Body mass	−0.840	0.331	−2.54	0.011
Cumulative winter severity index	0.914	0.302	3.03	0.003
Cumulative snow free days	−1.719	0.551	−3.12	0.002
Body mass:time	0.062	0.035	1.77	0.077

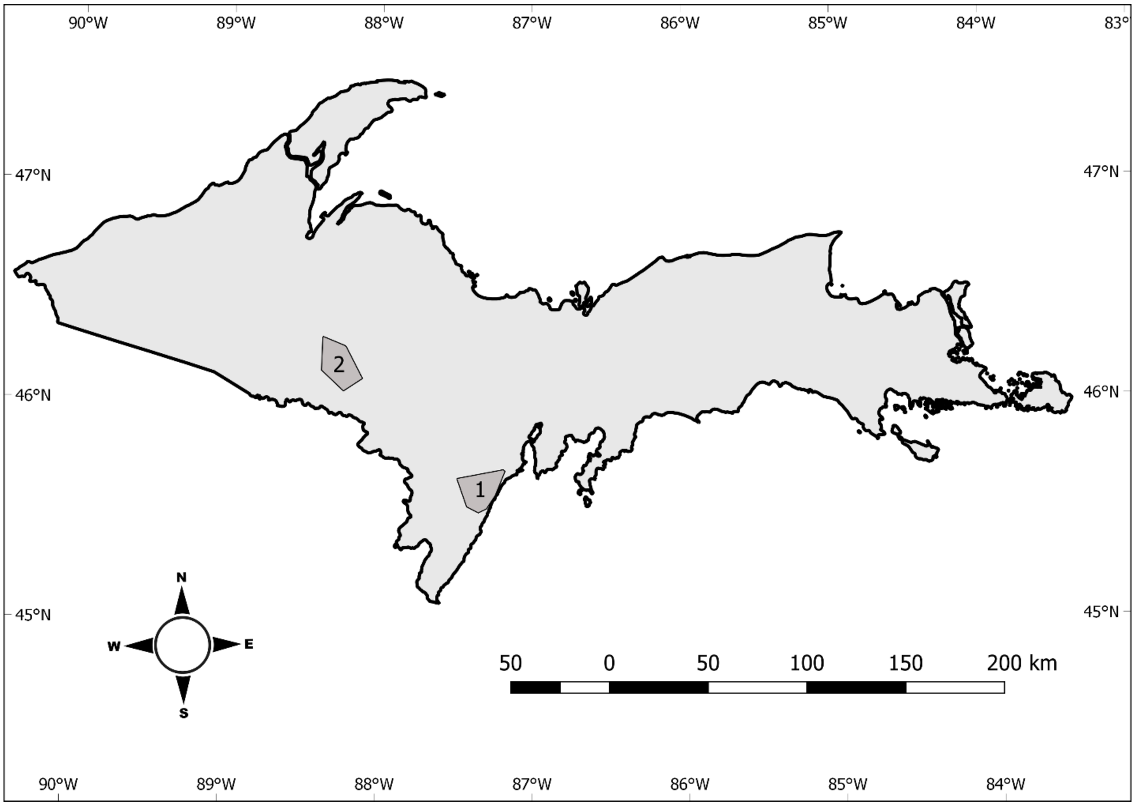

Figure 2.1 Location of low-snowfall (1) and mid-snowfall (2) study areas within the Upper Peninsula of Michigan, USA, 2009–2015.

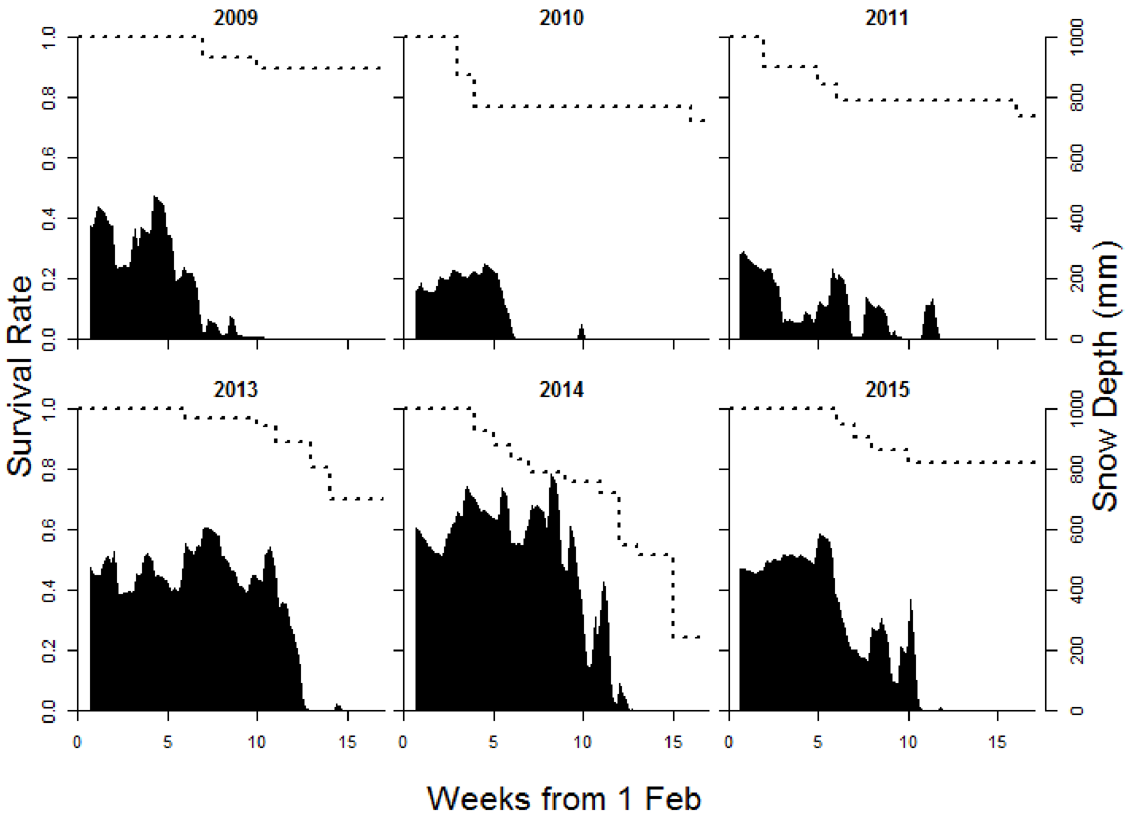

Figure 2.2 Weekly Kaplan-Meier survival estimates for adult female white-tailed deer (dotted line) and daily snow depth (shaded area) from 1 Feb to 31 May, Upper Peninsula of Michigan, USA, 2009–2015.

CHAPTER III

PREDATOR DENSITIES, KILL-RATES, AND BIRTH MASS DESCRIBE WHITE-TAILED DEER FAWN SURVIVAL IN A MULTI-PREDATOR SYSTEM

Introduction

In ungulate populations, juvenile survival generally has greater variability and influence on population growth than adult survival (Gaillard et al. 2000), with predation typically the primary mortality source for neonatal ungulates where predators are present (Linnell et al. 1997). Because high neonatal predation rates can result in population declines (Kilgo et al. 2012), understanding how predator species assemblages influence neonatal ungulate survival is important for managing wild ungulate populations. For white-tailed deer (*Odocoileus virginianus*), predation is the dominant mortality source for fawns <6 months old throughout North America (Gingery et al. 2018), although natural causes other than predation or anthropogenic causes can sometimes be a leading mortality source in areas where predators are present (Pusateri Burroughs et al. 2006, Warbington et al. 2017).

To date, most research on neonatal survival in white-tailed deer has occurred in systems with 3 or fewer predator species, typically American black bear (*Ursus americanus*), coyote (*Canis latrans*), and/or bobcat (*Lynx rufus*; Gingery et al. 2018). Yet, some areas of white-tailed deer range have > 3 predator species, indicating a need for further research in these systems. Griffin et al. (2011) reported North American elk

(*Cervus canadensis*) calf survival was reduced in areas with 4 or 5 predator species as opposed to 3. Additionally, density estimates for predator species are seldom reported in white-tailed deer fawn survival studies with 3 or more predator species present (e.g., Vreeland et al. 2004, Warbington et al. 2017). Estimates of cause-specific mortality attributed to predators are more meaningful when combined with predator density estimates, because this allows insights into kill rates (Gervasi et al. 2012).

Among the primary neonatal predators of white-tailed deer, 4 species are present in the Upper Peninsula of Michigan, USA: American black bear, coyote, bobcat, and gray wolf (*C. lupus*). Black bear predation on neonatal white-tailed deer and other ungulates is primarily opportunistic and generally occurs within the first weeks after birth (Zager and Beecham 2006). Coyotes are a generalist predator able to exploit many food sources to meet dietary needs (MacCracken and Hansen 1987), and neonatal ungulates are optimal prey for coyotes, especially when fawn mobility is limited (Sacks and Neale 2002). Indeed, in multi-predator systems throughout North America coyote predation tends to dominate white-tailed deer mortality during the first 6 months after birth (Gingery et al. 2018). Bobcats are obligate carnivores which may specialize in certain prey types regionally (Newbury 2013), but will generally exploit a range of species including white-tailed deer fawns (VanGilder 2008). Bobcat predation may be a predominant source of white-tailed deer fawn mortality in some areas (Roberts 2007, Kilburn 2018), but generally coyote predation exceeds bobcat predation in areas where both species are present (Gingery et. al. 2018). Wolves generally rely on ungulate prey for most of their diet, but can also derive a substantial portion of their diet from rodents, lagomorphs, domestic cattle, and other sources (Newsome et al. 2016). Although the typical optimal prey size for wolves (e.g. red deer [*Cervus elaphus*]; Jędrzejewski et al. 2002) is larger than a neonatal white-tailed deer fawn, wolves may switch foraging strategies during summer from killing fewer large prey items to killing greater numbers of small prey, including neonatal ungulates (Metz et al. 2012). Thus, based on their foraging habits, it is likely that each of these predator species would consume deer fawns when available. Yet, estimating the relative importance of each predator species as a fawn predator in a shared system is difficult because of differences in predator densities, along with the potential for differing kill rates of fawns among species.

In addition to the possible influence of predator species assemblages and densities on neonatal fawn survival, intrinsic factors within ungulate populations may also affect susceptibility to mortality from predation or other causes. For example, late-born neonatal ungulates may have increased mortality risk from predation or starvation (Clutton-Brock et al. 1987, Testa 2002, Kilgo et al. 2012). In some cases, fawns with lower body mass at birth were more susceptible to predation, starvation, or maternal abandonment (Verme 1977, Kunkel and Mech 1997). Finally, researchers have reported sex-biased differences in juvenile mortality in many vertebrates, including ungulates (Clutton-Brock et al. 1985).

Our goal was to measure fawn survival and cause-specific mortality risk from predation, other natural causes, and anthropogenic sources within a partially-migratory deer population sympatric with American black bear, coyote, bobcat, and wolf in the Upper Peninsula of Michigan, USA. We also examined the importance of intrinsic deer population factors of sex, birth mass, and timing of birth. Finally, we estimated densities of deer and predator species to provide context for the relative contribution of predators to fawn mortality. We predicted predation would be the primary mortality source for fawns due to the number of predator species present. We also predicted predator species with greater densities would consume more fawns at the population level because of increased opportunistic encounters or active foraging. We also predicted body mass of fawns would be negatively correlated with predation risk because smaller fawns are likely more vulnerable to predation. Finally, we predicted fawns born later in the season would be more susceptible to predation because predators would have refined search images to locate fawns, while earlier-born fawns would have greater mobility to avoid predators.

Study Area

The study area included 1,000 km2 within the Upper Peninsula of Michigan (46°14'00" N 88°13'00" W; Fig. 3.1). Mean annual precipitation was 52 cm of rain and 179 cm of snow (1951–1980 averages, Michigan Climatology Office 2013). Mean Jan and Jul temperatures were 13° C and 18° C, respectively (PRISM Climate Group 2016). Land cover was predominantly deciduous forest (38%), woody wetland (29%), mixed forest (13%), and evergreen forest (6%) (Fry et al. 2011). Deer predators include black bear, coyote, bobcat, and wolves. As moose occur at low density (~2/100 km2; D. Beyer, unpublished data), deer are the primary ungulate prey species available in Michigan's Upper Peninsula (Delguidice et al. 2009).

Methods

Population density estimates

We estimated deer densities during Aug–Sep each year using occupancy modelling derived from unmarked deer observed at 64 baited camera sites within an 8 x 8 grid with 6.25 km2 cells spaced >2.0 km from the nearest neighboring site to avoid detecting the same deer at multiple sites. We baited sites with 7.5 L of whole kernel corn at 3-day intervals during the 10-day pre-baiting period and 10-day survey. Cameras recorded 1 image when triggered at 5-minute intervals and we categorized deer in images as adult female, fawn, or adult male. We estimated abundance of adult female deer from daily occupancy of unmarked individuals along with space use estimates from radio-collared deer, using the Royle-Nichols model (Royle and Nichols 2003) fit to a Poisson distribution in the function OccuRN within package unmarked (Fiske and Chandler 2011) for program R (R version 3.4.1, www.r-project.org, accessed 15 Mar 2018; Duquette et al. 2014). We extrapolated abundance estimates at camera sites to density by assuming a detection radius equivalent to the average adult female home range during the survey interval (Keever et al. 2017), which we estimated to be 1.02 km^2 by calculating the 95% fixed kernel home range of 31 VHF and GPS collared adult female deer within the study area during 10–31 Aug 2015 (J. Belant, unpublished data).

We estimated the number of fawns born each year from the adult female deer density estimates from the fall camera survey by assuming an average fecundity of 1.41 fawns per doe ≥1 year old. We were confident adult female deer densities during the camera survey reflected adult female densities during May–Jul parturition because apparent survival of 118 radio-collared adult (≥2 years old) female deer within the study was 99.1% from 20 May to 6 Sep during 2013–2015 (J. Belant, unpublished data).

To reach the assumed fecundity of 1.41 fawns per doe, we estimated the proportion of 1, 2, and ≥3 year-old female deer within the population and calculated a weighted average fecundity based on published fecundity rates for each age class from the Upper Peninsula of Michigan (Verme 1969, Ozoga 1987). We estimated that 1- and 2-year-old deer comprised 13% and 11% of the adult female population, respectively, based on cementum annuli age estimates from 133 winter captures of adult female deer within the study area during 2013–2015 (J. Belant, unpublished data). We used average birth rates of 1.13 fetuses per doe for 2 year-old deer and 1.69 fawns per doe for ≥3 year old deer based on white-tailed deer fecundity ranges within Michigan's Upper Peninsula of 1.58–1.80 fawns/doe for female deer ≥3 years old in Jun, and 0.62–1.63 for females 2 years old in Jun (Verme 1969). Although deer commonly breed as fawns in some parts of the Midwest (e.g. Southern Michigan; Verme 1989), fertility of doe fawns in the Upper Peninsula is <1% even with maximum nutritional intake (Ozoga 1987), so we considered 1-year-old deer to be non-reproductive in our study area.

We estimated black bear density via non-invasive genetic sampling combined with spatial capture-recapture modelling (Efford 2004, Royle et al. 2014). For bears, we collected samples at 64 hair-snare sites within 6.25 km2 grid cells, checked on 5 occasions at 10-day intervals during May–Jul 2013–2015 (Fig. 3.1). Each site consisted of a single strand of 4-pronged barbed wire placed around 3–4 trees 50 cm above ground to create an enclosure. We baited snares by placing 0.5 L of fish oil on a pile of dead wood in the center of each enclosure and sprayed anise or raspberry oil on each of the trees 2 m above ground. Sample collection and handling procedures for black bear hair-snares followed those described by Belant et al. (2005).

We sampled bobcats using 64 break-away hair snare sites within 6.25 km^2 grid cells, checked on 8 occasions at 7-day intervals during 5 Jan–8 Mar 2013–2015 (Fig. 3.1). Each site consisted of an enclosure built with brush containing 4 openings at which snares were set (Stricker et al. 2012). Sites were baited using partial white-tailed deer carcasses obtained from local game processors, or whole skinned beaver carcasses. Baits were replaced each 7 days, as needed. Each site was lured with commercial lure placed on a tree 2 m above ground. Sample collection and handling procedures for bobcat hair-snares followed those described by Stricker et al. (2012).

Multilocus genotyping of black bear and bobcat hair samples was performed by Wildlife Genetics International (Nelson, BC, Canada) using 7 loci to identify individual bears and 8 loci to identify individual bobcats. From genetic samples, annual black bear and bobcat density was estimated using an open population spatial capture-recapture model (Gardner et al. 2010, Whittington and Sawaya 2015). Spatial capture-recapture models use individual and trap level detection data to estimate density while accounting for imperfect detection (i.e., the probability that individuals in the population are not detected during sampling), as well as variation in the probability of detecting individuals stemming from their differential exposure to sampling effort. Open population SCR models can be used to analyze multiple surveys, allowing for populations to change (i.e., animals to die and be recruited) between surveys. In addition to survey specific estimates of density, these models estimate survival probability and recruitment rate. SCR models include estimating the location of individual activity centers (conceptually, the average location of an individual during a survey); open population SCR models, therefore, also need to describe how activity centers change over time. We opted for a model where activity centers remain fixed across all three surveys, because this model is parsimonious and was shown to perform well for short time series (Gardner et al. *in press*). We implemented models in a Bayesian framework, using the software JAGS (Plummer 2003), accessed through R v. 3.4.1 (R Core Team, R version 3.4.1, www.r-project.org accessed 2017) using the package rjags (Plummer 2016).

We estimated coyote density during Jul–Oct, 2013 and 2014, using occupancy modelling derived from howl responses at 40 sites during 8 survey occasions conducted at 10-day interval (Fig. 3.1). We assumed a 2-km detection radius and buffered sites with a non-overlapping 3 km radius to avoid detection of the same individual at multiple sites during a survey (Petroelje et al. 2013). At each survey occasion, we broadcasted a pre-recorded coyote group-yip howl and defined a detection as at least one individual coyote response. From binary detection/non-detection data, we fit an abundance mixture model (Royle and Nichols 2003) within package unmarked (Fiske and Chandler 2011) for program R (R version 3.4.1, www.r-project.org, accessed 15 Mar 2018) with date as a covariate of detection and proportion of forest and herbaceous cover (Jin et al. 2013) as a covariate of abundance. Sampling and statistical analysis methods followed those described by Petroelje et al. (2013).

We identified wolf packs residing in a 1000 km^2 section of the study area using pack movements from GPS locations of collared individuals during 2013–2015, along with VHF collar data from long-term wolf population monitoring (D. Beyer, unpublished data). Wolves were fitted with GPS collars (model Lotek 7000SU GPS, Lotek Wireless, Newmarket, Ontario, Canada), which collected GPS locations at 15-minute intervals from May–Oct. From GPS locations, we calculated pack home ranges using a 95% fixed-kernel estimator within package adehabitat (Calenge 2006) for Program R (R version 3.4.1, www.r-project.org, accessed 15 Mar 2018) . We estimated wolf density each year during Jan–Mar using repeated track surveys within each wolf pack in the 1000 km^2 wolf survey area (Fig. 3.1; Becker et al 1998, Beyer et al. 2009).

Fawn capture and monitoring

We captured fawns during May–Jul 2013–2015 using gridded searches at birth sites determined from adult female deer with vaginal implant transmitters (VIT; model 3930, Advanced Telemetry Systems Inc., Isanti, MN, USA) and opportunistic encounters which occurred primarily along roads and trails. Birth dates of fawns captured using VITs were known, and birth dates of fawns captured opportunistically were estimated by measuring hoof growth at capture and back-calculating birth date using the equation described by Sams et al. (1996a). Body mass at birth was considered to be the same as capture mass for fawns <1 day old. For fawns known or estimated to be >1 day old, birth mass was estimated by subtracting an average neonatal white-tailed deer mass gain rate of 0.2 kg/day (Carstenson et al. 2009). Each fawn was fitted with an expandable VHF collar with 8-hour mortality switch (model 4210, Advanced Telemetry Systems, Inc., Isanti, MN, USA), and released at the capture site.

We monitored fawn survival daily using ground and aerial telemetry from capture until 31 Aug, then weekly from 1 Sep to 31 Dec. When a collar mortality signal was detected, we determined cause of mortality based on remains and evidence found at the site. For predation events, we determined predator species using sign (e.g., tracks, scat, carcass hemorrhaging, and site disturbance). We considered mortalities as predation based on the presence of hemorrhaged wounds, but in some cases fawns were nearly completely consumed with only a few bone shards or portions of hide remaining. Therefore, we also classified mortalities as predation if the time elapsed between mortality and investigation was <48 hours and predator sign was present at the site, but carcass remains were too scant to detect fatal wounds. We classified mortalities as unidentified predation in cases where predation was indicated as the cause of mortality but sign at the site did not indicate a single predator species, or indicated that multiple predator species had visited the carcass.

Fawn survival models and kill rate estimates

We assessed factors that could influence fawn weekly survival from birth to 26 weeks of age using mixed-effects Cox proportional hazards regression models in the package survival (Therneau 2018) for program R (R version 3.4.1, www.r-project.org, accessed 15 Mar 2018) . We divided known fates into three competing risk categories: 1) predation, including mortalities classified as predation by a known or unidentified predator species; 2) other natural causes, including mortalities attributed to starvation, maternal abandonment, disease, exposure, or unidentified natural non-predation; and 3) anthropogenic causes consisting of mortalities attributed to vehicle collisions.

For each competing risk category, we included individual covariates for date of birth (formatted as Julian day within each year), birth mass, and sex. We also included a random effect for year of birth within each model to account for various environmental factors (e.g. weather, vegetative phenology) which were not represented in our model but likely resulted in annual cohort survival effects. We established statistical significance at $\alpha < 0.05$. We calculated effect sizes of significant covariates in respective global models to assess their importance in explaining fawn survival.

We estimated population level kill rate for each predator species by extrapolating proportions of species-specific predation mortality from the collared fawn sample to the estimated density of fawns born. Fawn mortality rates were estimated using a Kaplan-Meier estimator within package survival (Therneau 2018) for program R (R version 3.4.1, www.r-project.org, accessed 15 Mar 2018). We then estimated the per-individual predation rate for each predator species by dividing the population level kill rate by the estimated density of that predator species (Swenson et al. 2007). Because fawn mortality sample sizes were small within years, we computed kill rates using the average predator densities during 2013–2015 and pooled fawn mortality among years. Consequently, estimated kill rate for each predator species represented the period average during 2013–2015.

Results

Population density estimates

We obtained 8,192 images of adult female deer and detected adult female occupancy on 68%, 56%, and 52% of survey days at baited camera sites during 2013, 2014, and 2015, respectively. Adult female density estimates ranged from 210/100km^2 to 260/100km2 (Table 3.1). Corresponding fawn density estimates ranged from 299/100km^2 to 367/100km^2 (Table 3.1).

During 2013–2015, we collected 584 hair samples from bobcat hair snares, of which 269 were identified as bobcat through genetic analyses. We detected 29 individuals (14 female, 15 male) 62 times. Twenty-two individuals were detected in one year only, and 7 individuals were detected in two or more years. Number of detections for individuals within year ranged from 1 to 5. Estimated bobcat density increased from 2.35/100km^2 in 2013 to 5.39/100km^2 in 2015 (Table 3.1).

During 2013–2015, we collected 1,296 black bear hair samples from black bear hair snares, from which genetic analyses identified 238 unique bears (117 females, 212 males); 171 were detected in one year only, 42 were detected in 2 years, and 24 in 3 years. Number of detections for individual bears within year ranged from 1 to13. Estimated bear density was similar over years ranging from 23.2/100km^2 in 2014 to 28.8/100km^2 in 2015 (Table 3.1).

We detected coyote responses on 25.0% and 31.5% of howling occasions and detected coyotes at least once at 83% and 85% of survey sites during 2013 and 2014, respectively. Estimated detection (10.0% during 2013 and 2014) was not influenced by date. Estimated coyote abundance was not influenced by proportion of forest or herbaceous cover and was similar at 23.1/100km^2 in 2013 and 24.4/100km^2 in 2014 (Table 3.1).

We identified 5 wolf packs each year of the study. We captured 4 wolves during 2013, 5 wolves during 2015, and 4 wolves during 2015 such that 4 of the packs present had ≥1 individuals GPS-collared from Jun–Sep during ≥1 years of the study. VHF telemetry was used to define the home range of home one pack which not have any GPS-collared individuals during the study period. We estimated a mean of 5.6 individuals/pack (SD = 1.8 individuals). Mean estimated annual wolf density was 2.80 individuals/100km^2 and did not change during 2013–2015 (Table 3.1).

Fawn capture and monitoring

We captured and radio-collared 100 fawns (42 females, 58 males), with 43, 25, and 32 fawns captured during 2013, 2014, and 2015, respectively. Of these, 37 fawns were captured using VITs and 63 were captured opportunistically. Mean estimated birth mass of fawns was 3.1 (95% CI = 2.8–3.4) kg during 2013, 3.5 (95% CI = 2.9–4.1) kg during 2014, and 3.1 (95% CI = 3.5–4.4) kg during 2015. Average fawn birth date among years combined was 7 Jun.

Overall 6-month fawn survival was 39% (95% CI = 30–51%; Fig. 3.2), and within year survival was 20% (95% CI = 9–46%) during 2013, 58% (95% CI = 41–82%) during 2014, and 42% (95% CI = 28–64%) during 2015. Fifty-six mortalities were documented, which included 11 coyote predations, 11 black bear predations, 6 bobcat predations, 4 wolf predations, 13 unidentified predations, 3 weak fawn syndrome, 1 maternal abandonment unrelated to capture, 1 pulmonary edema, 3 vehicle collisions, and 3 unidentified trauma (Table 3.2). Most (76%) predations occurred within 6 weeks of birth (Fig. 3.3). Twenty-two fawns were censored within survival analyses as a result of failed collar attachment hardware that caused collars to drop off (*n* = 9), slipped collars (*n* = 10) or radio-collar signal loss (*n* = 3). Mean age at time of censor was 10.6 weeks (SD = 7.5 weeks).

Fawn survival and kill rate estimates

Our mortality event sample sizes for competing risk categories were 45 for predation, 8 for other natural causes, and 3 for anthropogenic causes. From model estimates, the only significant relationship was between birth mass and predation risk, where risk of mortality due to predation decreased by 24% (95% CI = 1–43%; P = 0.048) with each 1 kg increase in birth mass relative to the population average (Table 3.3).

Extrapolating from radio-collared fawn mortality and deer/predator density estimates, we estimated that black bear, coyote, bobcat, wolf, and unidentified predation accounted for the fates of 12%, 12%, 7%, 4%, and 14%, respectively, of the total fawn population. Estimated individual kill rates of fawns from birth to 26 weeks (6 months) was 1.6 fawns/black bear, 1.7 fawns/coyote, 5.5 fawns/bobcat, and 5.2 fawns/wolf. At the population level, the minimum annual estimated fawn consumption by predator species was 40.0 fawns/100 km^2 for black bear, 40.0 fawns/100 km^2 for coyote, 21.8 fawns/100 km^2 for bobcat, and 14.6 fawns/100 km^2 for wolf.

Discussion

As we predicted, predation of fawns was the dominant source of mortality and accounted for 80% of all deaths. This is largely consistent with studies of white-tailed deer and other ungulate species where predators are present (Linnell et al. 1997, Gingery et al. 2018). In Louisiana, Shuman et al. (2017) found that a 3-predator system had fawn predation rates similar to those in 2-predator systems in the southern United States, and suggested there may be an upper limit to predation rates on white-tailed deer fawns at which additional predator species have little effect. Our results lend support to their hypothesis and despite the presence of 4 predator species in our study area, our overall fawn survival from birth to 6 months old of 39% was similar to the average estimated white-tailed deer survival from birth to 3–6 months of 41.4% within North American forested landscapes (Gingery et al. 2018). Predation rates on white-tailed deer fawns vary among species within the same predator assemblage. In northern Wisconsin, the greatest proportion of known-predator fawn kills was attributed to black bear, followed by bobcat and coyote, with no fawn mortalities attributed to wolf despite numerous wolf packs within their study area (Warbington et al. 2017). In the southcentral Upper Peninsula of Michigan, most fawn mortality was attributed to coyote, followed by bobcat, and finally black bear and wolf (Duquette et al. 2014). Considering that our study and these previous studies (Duquette et al. 2014, Warbington et al. 2017) contained the same 4-species predator assemblage and occurred within 300 km of each other, the observed differences among predator species contributions to fawn mortality warrants further investigation. Differing fawn predation patterns in multiple systems with the same predator species are likely related to the densities of predators and fawns, the kill rates of predators, or both (Gervasi et al. 2011, Melis et al. 2013, Kilgo et al. 2014). We recommend future studies of cause-specific mortality of deer or other prey species estimate predator and prey densities to improve our mechanistic understanding of variation in predation rates.

Twenty-nine percent of fawn predation mortalities were not accounted for in our estimates of kill rates because we were unable to identify the predator species involved. Consequently, our reported fawn kill rates for predator species are minimum estimates. The extent to which kill rates were underestimated may vary among predator species due to bias in identifying predator species with sign left at the carcass. For example, bobcats may be more likely to be identified at a kill site because they often return to the carcass multiple times to feed (Beale and Smith 1973) and have distinct habits of covering carcasses with plucked fur and scraped debris in many cases (Labisky and Boulay 1998). We observed that black bear kill sites were often easily identified by sign because they are large and leave identifiable tracks in most substrates, and often left one or more scats at kill sites. Coyotes and wolves have relatively light foot-loading (Telfer and Kelsall 1984), making tracks unlikely to register in many substrates. At kill sites with tracks present, coyotes and wolves in our study had similar consumption patterns of neonatal fawns where most of the carcasses were consumed while mandibles, long bones, and lower legs commonly remained; none of which were likely to have distinct canine puncture spacing. Therefore, distinguishing kills among coyotes and wolves was often difficult, and in 4 of 13 unidentified predations we determined the predator was a canid based on hair or scat, but could not determine which species. Consequently, we suspect most of the unidentified predator kills were by coyotes and wolves. Assuming the 13 fawns killed by unidentified predators were killed by coyotes and wolves in proportion to their known number of kills would result in 10 additional coyote kills and 3 additional wolf kills. The subsequent estimated proportion the total fawn population consumed by coyotes and wolves, respectively, would be 23% and 8%, the individual kill rates would be 3.2 fawns/coyote and 9.1 fawns/wolf, and the estimated fawn consumption (fawns/100 km^2) would be 76 and 25. Hence, even when accounting for the bias from unidentified predations, our conclusions regarding densities and kill rates hold in that coyotes and black bears were the most prevalent fawn predators while bobcats and wolves had the greatest estimated per-individual fawn kill rates.

Recent advances in identifying predators of neonatal deer using DNA swabs from carcass wounds have been effective (Kilgo et al. 2012, Shuman et al. 2017). Shuman et al. (2017) found a high level of agreement between predator species identified using DNA swabs and sign at the mortality site for black bears, coyotes, and bobcats, suggesting that using tracks, scat, and other sign at kill sites is reliable for identification for those species. However, we recommend that future cause-specific mortality studies in systems with coyotes and wolves use DNA-based evidence to reduce the number of unidentified predators at kill sites.

Coyote and black bear had low estimated per-individual kill rates, but existed at high densities which resulted in a large population-level contribution to fawn mortality. Black bears and coyotes are both generalist predators which have wide, omnivorous dietary niches (Litvaitis and Harrison 1989, Romain et al. 2013). Across North America, black bear predation of neonatal ungulates is opportunistic, and generally occurs in the first few weeks of life (Zager and Beecham 2006, Bastille-Rousseau et al. 2011). Nonetheless, bears can be an important source of neonatal ungulate mortality which can be additive (Griffin et al. 2011). Although coyotes would be expected to select neonatal ungulates over most other foods when available (Sacks and Neale 2002), coyotes adapt their foraging and target diverse prey items to maximize energetic return (MacCracken and Hansen 1987). In our study area fawns may not have been abundant enough to facilitate prey switching by coyotes, potentially exacerbated by the presence of three other predator species.

The individual bobcat kill rate was >3 times greater than black bears or coyotes, suggesting bobcat predation of fawns was not opportunistic. This result is contrary to previous studies where bobcats consumed less ungulate prey than sympatric coyotes during summer in Alabama, (VanGilder 2008), California (Neale and Sacks 2001), and Maine (Litvaitis and Harrison 1989). However, Svoboda et al. (2013) identified 37 fawn kills made by 7 bobcats during May–Aug 2009–2011 in the Upper Peninsula of Michigan, suggesting bobcats in this area may be more specialized at targeting neonatal deer than other bobcat populations. Wolves also had a greater estimated per-individual kill rate than black bears or coyotes in our study, and can specialize in hunting neonatal ungulates during summer (Metz et al. 2012, Newsome et al. 2016). Where wolves and coyotes co-occur, wolves tend to derive a greater portion of their diet from ungulate prey (Arjo et al. 2002, Benson et al 2017). Despite greater individual fawn kill rates by bobcats and wolves, the overall contribution to fawn mortality was low in comparison to black bears and coyotes, a consequence of low bobcat and wolf densities.

Contrary to our predictions and observations by Kilgo et al. (2012), we observed no effect of birth date on fawn mortality risk. This could be due to less variation in birth dates for deer in our study, where the average range of birth dates within years was 36 days, in comparison to an average range of 57 days reported by Kilgo et al (2012). Furthermore, most (82%) births in our study occurred within an 18-day period from 26 May to 14 Jun. Likely, this contracted birthing period is a consequence of winter weather in our study area; ungulates in northern climates often have a short optimal window for birth timing due to constraints of spring vegetative phenology set against necessary time for growth to survive winter as a juvenile (Gaillard et al. 1993, Cook et al. 2004).

The increased predation risk we observed for fawns with lower birth mass suggests predators had greater success in capturing weak fawns, supporting our prediction and previous studies demonstrating weaker individuals were more susceptible to predation (Errington 1946, Genovart et al. 2010). As white-tailed deer fawns which are small at birth are more likely to come from weaker mothers and tend to be smaller at 5–6 months of age (Michel et al. 2015, 2018), it is plausible birth mass remained correlated to fawn condition throughout the 6 month age class in which we monitored survival. White-tailed deer fawns with low birth mass can have increased mortality risk from predation

(Kunkel and Mech 1994) or combined causes (Verme 1977, Saalfeld 2006, Therrien et al. 2007, Shuman et al. 2012), but other studies have found no relationship (Grovenburg et al. 2012, Kilgo et al. 2012) or context-dependent relationships. Vreeland (2002) reported fawns with lighter birth mass were more susceptible to mortality overall, but found no relationship within predation mortality. Wright (2018) reported fawn mortality risk increased with lower birth mass for female fawns, but not male fawns. The slope of the relationship between fawn birth mass and mortality risk was lesser in our study (24% decrease in risk/kg) than that reported in Louisiana where predation was the dominant mortality source (81% decrease in risk/kg; Shuman et al. 2017), but both studies suggested reduced predation risk for larger fawns. Taken together, this evidence suggests a relationship between fawn birth mass and survival is context-dependent among white-tailed deer populations, but where such a relationship exists, smaller fawns are generally at greater risk of mortality.

White-tailed deer fawn predation rates tend to decline as fawns age, with the greatest decline within the first 3 weeks after birth (Vreeland 2002, Kilgo et al. 2012, Chitwood et al. 2015a). This suggests fawn growth and body size influence susceptibility to predation. The average daily rate of neonatal white-tailed deer fawn mass gain is 0.2 kg (Carstenson et al. 2009), and the standard deviation of birth mass for fawns in our sample for all years combined was 1.3 kg. Hence, variation in fawn birth mass within this population could represent up to 1 week of post-birth growth. Increased body size at birth may give fawns a “head-start” toward achieving a threshold of size and speed which facilitates predator escape. Additionally, fawns which are born weak may be more vocal and could be at increased risk of predation by attracting predators (Chitwood et al. 2014).

Wolves contributed little to fawn mortality in other areas with 4 predator species (Duquette et al. 2014, Warbington et al. 2017). In contrast, Kunkel and Mech (1994) attributed 51% of May–Oct white-tailed deer fawn mortality to wolf predation, and although the estimated wolf density within their study area was similar to ours (2.6 and 2.8 wolves/100 km2, respectively), their fawn survival sample was small (21 fawns, 9 mortalities). As wolves in our study area are not legally harvested and wolf densities in the Upper Peninsula have been stable since 2013 (O'Neil et al. 2017), our findings suggest observed wolf predation on fawns was at or near maximum levels for this area. Our estimated wolf density of 2.8 individuals/100 km2 was well within the range reported for North America, which can achieve densities ≥4 individuals/100 km^2 (Fuller et al. 2002). At higher densities, wolves may become a major fawn predator. Worldwide, wolf presence is correlated with reduced ungulate densities (Ripple and Beshta 2012), and wolves are a primary predator of older white-tailed deer (DelGuidice et al. 2002). Within our study area during 2013–2016, wolves accounted for 28% of all adult female deer mortality (J. Belant, unpublished data) and we suggest that wolf effects on white-tailed deer are primarily manifested through predation of deer >6-months old. In contrast, coyotes may limit deer populations through high predation rates on fawns <6 months old, even in areas where they rarely kill adult deer (Kilgo et al. 2012, 2016; Chitwood et al. 2015b).

Studies of white-tailed deer fawn survival sometimes report qualitative predator densities (e.g., Vreeland et al. 2004, Warbington et al. 2017), or provide quantitative data for only some predator species (e.g., Kunkel and Mech 1994, Kilgo et al. 2012, Shuman et al. 2017). We recognize the difficulties of simultaneously estimating deer and multiple predator densities but suggest that our understanding of predator-prey relationships will be limited unless studies include densities of predators and prey, particularly in multiple predator systems.

Although we did not observe any relationship between mortality risk from non-predation natural causes or anthropogenic causes, our sample sizes for these risk categories were small (8 and 3 mortalities, respectively). However, these risk categories were also relatively unimportant for fawns in our study when compared with predation (45 mortalities observed), which supports predation as the dominant mortality source in white-tailed deer fawn survival (Gingery et al. 2018). Where non-predation natural causes were an important source of fawn mortality, smaller birth mass tended to be associated with increased mortality risk from emaciation or disease (Verme 1977, Sams et al. 1996b). Considering these previous studies, our observation that smaller fawns tend to have greater mortality risk from predators suggests that predation may be partially compensatory to other natural causes of mortality for neonatal fawns in this population.

We were unable to determine at-birth fecundity rates and sibling status of fawns. Capturing multiple fawns from litters of white-tailed deer is difficult because fawns within litters are generally separated and can move >100 meters from the birth site within 13 hours post-parturition; even fawn searches conducted <12 hours postpartum are often unsuccessful at finding one or more fawns (Haskell et al. 2007). Although we captured at least one fawn from most implanted does, many sibling fawns likely were undetected. Similarly, only 2 of 61 opportunistic fawn captures consisted of twin fawns captured together. As litter size has been related to neonatal survival in other wild ungulates (e.g., mule deer (*O. hemionus*; Johnstone-Yellin et al. 2009), our limited ability to capture complete litters may have influenced our estimates of survival and cause-specific mortality.

Conclusions

Predation was the dominant source of mortality of white-tailed deer fawns from birth to 6 months, but was distributed among 4 predator species with no single predator species accounting for >34% of known-species predation mortality. Hence, manipulating the density of any single predator species will likely have limited effects on overall fawn survival. Furthermore, our results suggest that predator species with low per-individual fawn kill rates but high densities (i.e., coyote and black bear) may contribute more to fawn mortality than predator species with high per-individual kill rates and low densities (i.e., bobcat and wolf). Consequently, focusing efforts on coyotes or black bears will likely yield greater effects if predator removal is used as a strategy to increase fawn survival. Finally, because fawn birth mass was negatively correlated with predation risk, increasing the nutritional condition of deer within this population may result in lower fawn predation rates even if predator densities remain stable. Broad-scale habitat management strategies which increase the nutritional carrying capacity for deer may be the best option for managers to influence deer condition, because supplemental feeding of deer can increase risk of disease transmission at concentrated feed sites (Sorenson et al. 2014).

Table 3.1 Density estimates (individuals/ 100km2 [95% confidence interval]) for white- tailed deer and predator species, Upper Peninsula of Michigan, USA, 2013–2015.

Population	Year			
	2013	2014	2015	Average
White-tailed deer adult female	261 (194–384)	238 (172–334)	211 (158–320)	237
White-tailed deer fawn	368 (273–541)	336 (243–471)	298 (223–451)	334
Coyote	23.1 (10.4–51.9)	24.4 (11.5–51.9)	NA	23.8
Bobcat	2.4 (0.7–4.0)	4.3 (2.0–6.5)	5.4 (3.0–7.8)	4.0
Black bear	25.2 (21.2–29.2)	23.2 (19.7–26.7)	28.8 (24.6–33.0)	25.7
Wolf	2.8	2.8	2.8	2.8

Table 3.2 Known fates of 100 radio-collared white-tailed deer fawns from birth to 26 weeks old, Upper Peninsula of Michigan, USA, 2013–2015.

	Year			
Fate	2013	2014	2015	Pooled
Black bear	2	4	5	11
Coyote	6	2	3	11
Bobcat	2	1	3	6
Wolf	3	1	0	4
Unidentified predator	7	1	5	13
Abandonment	1	0	0	1
Pulmonary edema	1	0	0	1
Unidentified trauma	2	1	0	3
Weak fawn syndrome	3	0	0	3
Vehicle collision	1	0	2	3
Censored	12	6	4	22
Survived period	3	9	10	22
Total	43	25	32	100

Table 3.3 Estimates of fawn mortality risk from 100 radio-marked fawns in response to birth mass, sex, and date of birth, Upper Peninsula of Michigan, USA, 2013–2015.

	Competing risk model (*n* events observed)								
	Predation (45)			Other natural causes (8)			Anthropogenic (3)		
Covariate	β	SE	*P*	β	SE	*P*	β	SE	*P*
Birth mass	-0.28	0.14	0.048	-0.09	0.24	0.710	0.24	0.44	0.580
Sex male	-0.19	0.31	0.550	0.89	0.67	0.180	0.61	1.26	0.630
Date of birth	0.00	0.02	0.780	0.01	0.03	0.690	0.37	0.67	0.580

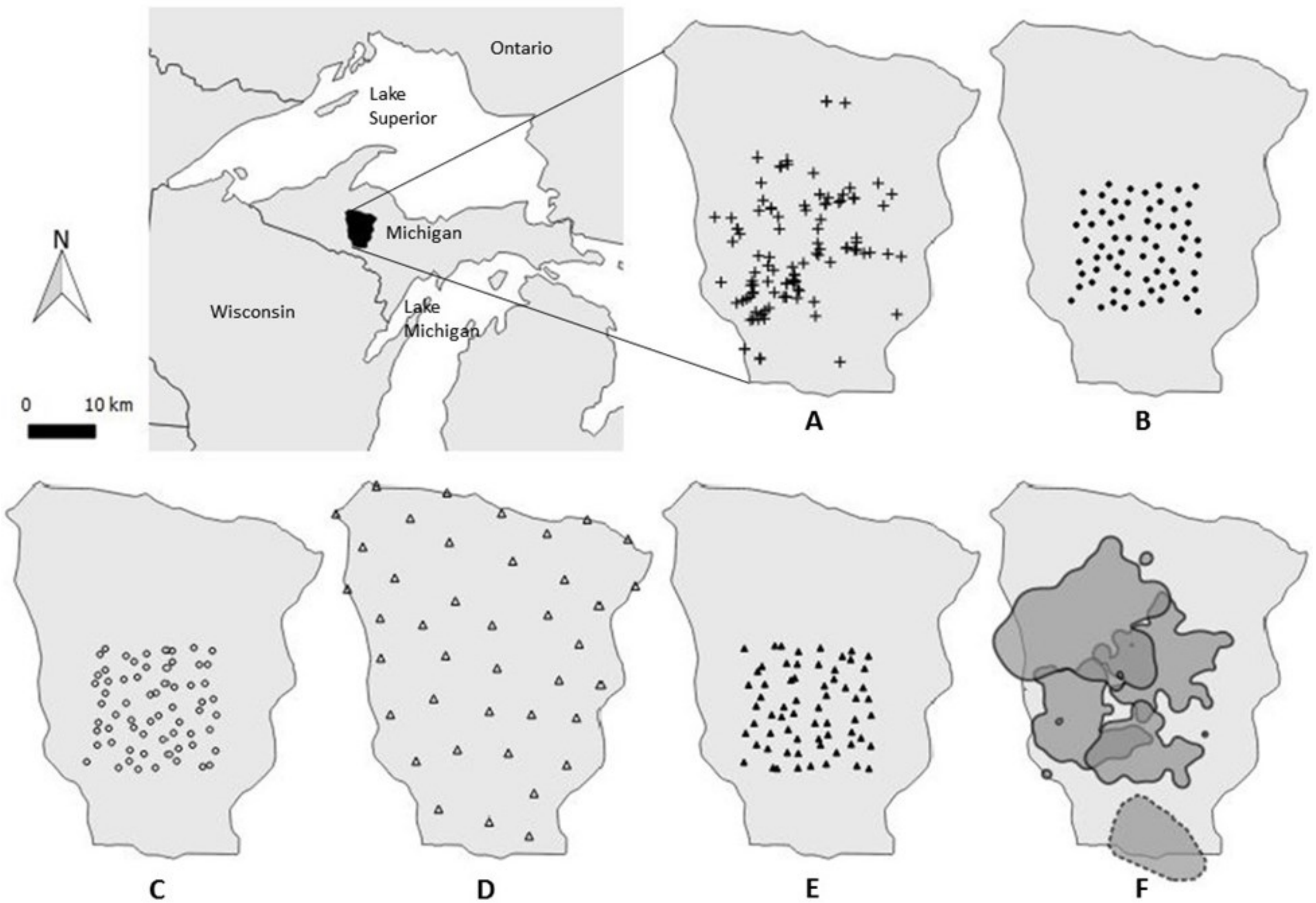

Figure 3.1 Locations of white-tailed deer fawn capture sites (A), deer camera survey sites (B), black bear hair snare sites (C), bobcat hair snare sites (D), coyote howl survey sites (E), and 95% utilization distribution fixed kernel home ranges of 4 wolves (solid outlines) along with historic VHF telemetry range of one pack (dotted outline) representative of packs used for track surveys (F), Upper Peninsula of Michigan, USA, 2013–2015.

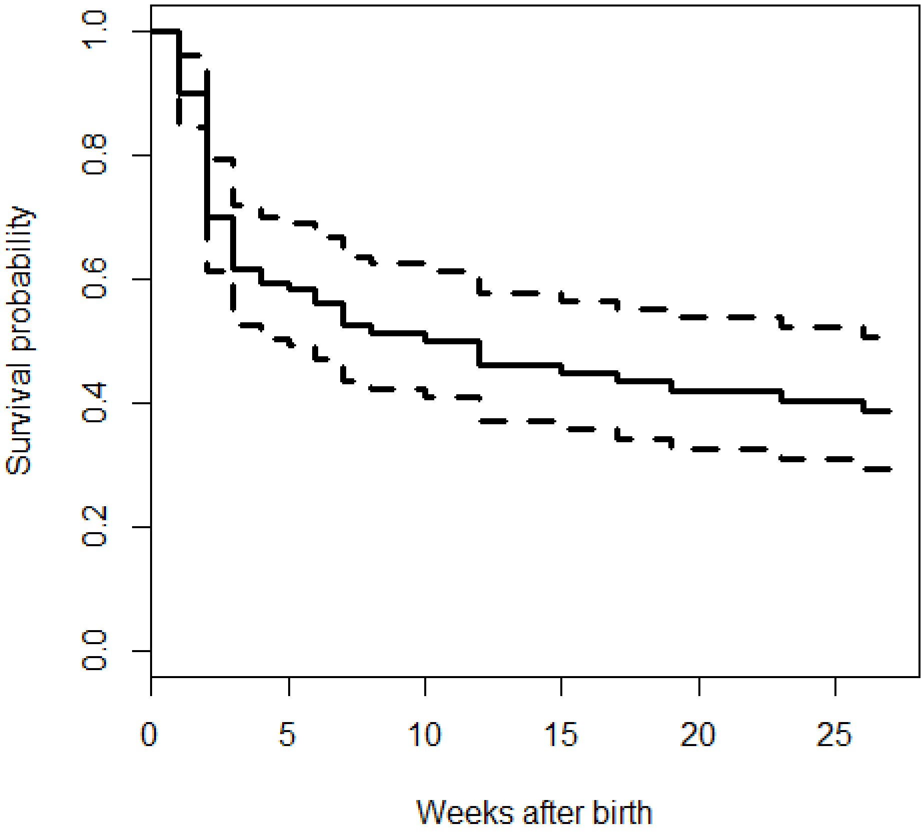

Figure 3.2 Kaplan-Meier survival probability from birth to 26 weeks old for 100 radio-collared fawns, Upper Peninsula of Michigan, USA, 2013–2015. Dashed lines represent 95% confidence intervals.

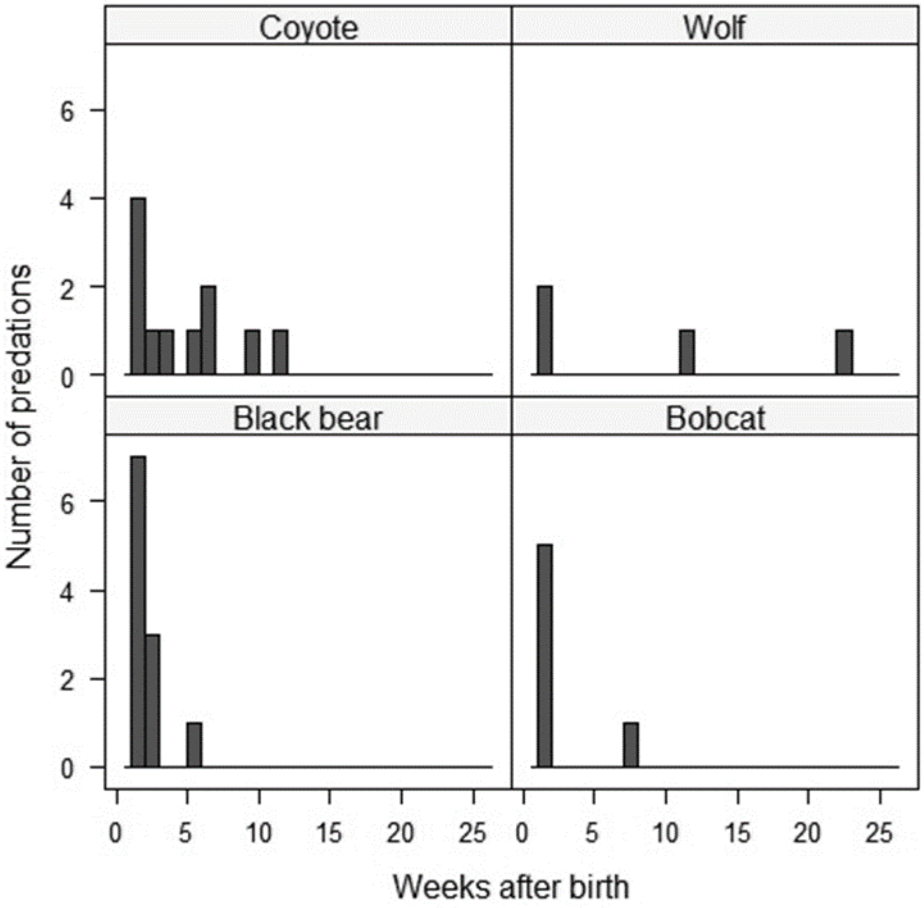

Figure 3.3 Weekly number of predations by predator species for 100 white-tailed deer fawns from birth to 26 weeks old, Upper Peninsula of Michigan, USA, 2013–2015.

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