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SURVIVAL, MOVEMENTS, AND RESOURCE SELECTION OF FEMALE WHITE-TAILED DEER IN MISSOURI

By

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Thesis

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Survival, movements, and resource selection of female white-tailed deer in Missouri

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ABSTRACT

White-tailed deer (*Odocoileus virginianus*) in Missouri are a socially and economically important game species generating annual revenue in excess of $1 billion. The last comprehensive deer study in Missouri was conducted in the 1980s – 1990s when deer populations were rapidly expanding. Since this time there has been a reduction in deer population size, declining growth rates, changes in harvest strategies, and the emergence and spread of chronic wasting disease (CWD). These changes have rendered prior survival estimates outdated, and the presence of CWD requires a deeper understanding of movement patterns and space use. We were interested in providing updated deer survival rates, and quantifying how deer altered their movements and resource selection during two critical time periods in the Glaciated Plains (GP) and Ozarks (OZ) eco-regions. Two contrasting study areas allowed us to understand how land use and ownership, harvest regulations, and habitat composition and fragmentation affected deer survival and behavior.

In Chapter 1 we estimated neonate (≤ 16 weeks old) survival rates and determined how habitat characteristics influenced neonate survival. In Chapter 2 we investigated how pregnancy, parturition, and lactation affected deer movement behaviors and resource selection. In Chapter 3 we estimated annual female fawn (> 6 months, but < 1 year old), yearling (1 year old), and adult (≥ 2 years old) survival rates, and investigated how the hunting season affected female movement behaviors and resource selection. Survival rates of all age classes were similar between the two eco-regions, with neonate survival rates between 0.40 – 0.50, and survival rates for females > 6 months old between 0.80 – 0.90. Females in both study areas altered their movements similarly in response to parturition, and selected for conservation reserve program grasslands in the GP, and forest habitat in the OZ during pregnancy and lactation. Females in both study areas increased their movements during the hunting season, and altered their resource selection after the hunting season, suggesting that breeding behaviors and resource availability were influencing deer behavior during this time period.

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To recognize the input, support, and field assistance provided by everyone above I use the term we, instead of I throughout this thesis.

Chapter 1: Effects of landscape scale habitat characteristics on the survival of neonatal white-tailed deer (*Odocoileus virginianus*) in two different eco-regions of Missouri

ABSTRACT

Landscape level habitat characteristics affect neonatal white-tailed deer (*Odocoileus virginianus*) survival throughout their distribution. However, little is known about how changes in dam habitat use affect neonate survival or how landscape patterns affect neonate survival. We quantified survival rates and determined if neonate survival was affected by weekly dam habitat use in the highly fragmented Glaciated Plains (GP) and more contiguous Ozark (OZ) eco-regions of Missouri. We captured 111 pregnant female deer from January – March 2015-17, fitted them with global positioning satellite (GPS) radio-collars and implanted vaginal implant transmitters (VIT). We captured 226 neonates during May – June 2015-17, fitted them with expandable radio-collars and monitored survival status daily. We created weekly dam home ranges and calculated habitat metrics within these home ranges. We used the Kaplan-Meier estimator to calculate 8-week survival estimates and Cox proportional hazards models to investigate the influence of habitat covariates on survival. The 8-week survival estimates were 0.43 (95% CI: 0.35 – 0.54) and 0.47 (95% CI: 0.39 – 0.58) in the GP and OZ, respectively. The null model fit best in the GP, and a sex x birth mass interaction fit best in the OZ. Additional modeling using habitat variables indicated that in the GP, increasing the landscape shape index (LSI), or amount of edge, by 1 unit increased neonate mortality risk by 1.6 times (95% CI = 1.12 – 2.29), increasing patch shape complexity by 1 unit increased mortality risk by 2.94 times (95% CI = 1.22 – 7.17), and increasing forest patch size by 1 ha increased mortality risk by 1.28 times (95% CI = 1.04 – 1.57) but only until neonates were about 2 weeks of age. In the OZ, increasing the percentage of grassland within the dams' home range by 1% decreased neonate mortality risk by 2% and increasing grassland patch density by 1 patch per 100 ha increased neonate mortality risk by 22%, but only until neonates were 2 weeks of age. Although we did not conclude that predation was the leading cause of mortality in our study, it is likely these metrics are related to predator searching efficiency and abundance. Habitat metrics that influenced survival in the OZ described the amount and spatial configuration of a specific habitat type, while metrics that affected survival in the GP described the spatial configuration of the landscape. Perhaps in more fragmented and diverse areas, where different habitat patches are well interspersed, the spatial configuration of the landscape affects neonate survival more than the amount of any specific habitat type.

KEY WORDS white-tailed deer, neonate, survival, Missouri, *Odocoileus virginianus*, habitat, home range.

INTRODUCTION

Neonatal white-tailed deer (*Odocoileus virginianus*) survival rates contribute greatly to population growth rates because they are the life stage most susceptible to mortality and experience the greatest temporal variability (Gaillard et al. 1998, DelGiudice et al 2006, Chitwood et al. 2015*a*). Survival of neonates is affected by many biological and environmental conditions including winter severity (Duquette et al. 2014), habitat (White et al. 2010), and predators (Ballard et al. 2001). These factors are often interrelated and can affect survival directly (Chitwood et al. 2015*b*) or indirectly through maternal nutritional condition, which can impact neonate growth rates and ultimately survival (Carstensen et al. 2009, Duquette et al.

2014, Shallow et al. 2015, Long et al. 2016). In addition, annual weather conditions can also impact the degree to which these factors affect neonate survival (Griffin et al 2011). Identifying and understanding the limiting factors causing variation in neonate survival is important to understanding white-tailed deer population dynamics and making management decisions (Roseberry and Woolf 1991, Bowden et al. 2000, Lubow and Smith 2004).

Habitat plays an important role in neonate survival by influencing the use of resources by dams, which affects maternal condition (Therrien et al. 2008, Duquette et al. 2014, Shallow et al. 2015), and by influencing the density, searching efficiency, and distribution of predators (Gese et al. 1996, Rohm et al. 2007). Neonates reduce their susceptibility to predation by selecting bed sites that have dense ground cover with low visibility or are on steep slopes (Fox and Krausman 1994, Piccolo et al. 2010, Pitman et al. 2014). Some studies did not find a strong relationship between these microhabitat bed site characteristics and neonate survival (Hyde et al. 1987, Kilgo et al. 2014, Chitwood et al. 2015*b*). However, survival is a complex process and can be influenced by habitat types and the configuration of habitat types at varying spatial scales (Andrén 1995, Brown and Litvaitis 1995, Coulson et al. 1997). For example, Van Moorter et al. (2009) found that neonate roe deer (*Capreolus capreolus*) survival was influenced more by the availability of high quality habitat within the does' home range than by the bed site selected by the neonate.

In France (Pettorelli et al. 2005) and the Midwest (Rohm et al. 2007, Grovenburg et al. 2012*a*, Jacques et al. 2015) and Southern (Gulsby et al. 2017, Shuman et al. 2017) regions of the United States, researchers found that habitat variables at a large spatial scale influenced neonate ungulate survival. Amount of edge (Rohm et al. 2007, Van Moorter et al. 2009, Gulsby et al. 2017) and metrics related to cover habitat (Rohm et al. 2007, Grovenburg et al. 2012*a*, Jacques et al. 2015, Shuman et al. 2017) are the two most common landscape-scale habitat characteristics that influence neonate survival, but much variation exists. For example, Grovenburg et al. (2011) did not find any relationship between habitat characteristics and neonate survival in southwestern Minnesota and eastern South Dakota, but Grovenburg et al. (2012*a*) did find a significant relationship only 150km away in north-central South Dakota. These contrasting results highlight the complex relationship between habitat, localized predator densities, year to year variation, and neonate survival, and the difficulty in extrapolating results from one region to another.

Two different methods have been used to determine the appropriate spatial scale at which to calculate habitat metrics. Neonate capture locations were either buffered by mean female summer home range size (Van Moorter et al. 2009, Grovenburg et al. 2011) or a mean neonate home range size (Rohm et al. 2007, Grovenburg et al. 2012*a*, Jacques et al. 2015, Gulsby et al. 2017). Both of these spatial scales make biological sense because neonates move independently of the dam (White et al. 1972) but this movement is closely linked to the dams' space use (White et al. 1972, Ozoga et al. 1982, Schwede et al. 1993). However, due to limitations in collecting location data with very high frequency (VHF) collars at a fine temporal scale, these studies may have failed to incorporate how temporal variation in space use could affect neonate survival. As neonates age they become more mobile and increase their space use (DeYoung and Miller 2011), maternal doe home range size increases (Chapter 2), and both doe and neonate resource selection changes (Long et al. 2009, Van Moorter et al. 2009). Using one spatial scale for the entire neonate period could oversimplify the space use of neonates and does, which in turn could lead to incorrect conclusions about the relationship between habitat and neonate survival.

We were interested in better understanding the relationship between white-tailed deer neonate survival rates and temporal variation in habitat use, and how this relationship might differ between different geographic regions. We conducted our research in two distinct eco-regions of Missouri, the Glaciated Plains (GP) and Ozarks (OZ), which encompass the northwest and south-central regions of the state, respectively. The GP is dominated by row-crop agriculture with the forested habitat being highly fragmented, while the OZ is dominated by large contiguous tracts of forest. Having two distinct study areas allowed us to investigate how the broader context of habitat, land use, and fragmentation affected neonate survival.

We were also interested in estimating 8 and 16-week survival rates for neonatal white-tailed deer in Missouri. Survival rates for neonates in Missouri were last collected in the late 1980s and early 1990s when deer populations were growing rapidly. However, since this time there have been numerous changes to the deer population including a reduction in deer population size, declining growth rates, changes in harvest strategies, and the emergence and spread of chronic wasting disease (CWD), rendering these prior estimates outdated for use in population models and current management plans (Missouri Department of Conservation [MDC] 2015). Thus, our objective was to provide updated estimates of neonate survival to assist with ongoing white-tailed deer management in Missouri, while evaluating the effects of habitat on neonatal survival in 2 disparate eco-regions of the state.

STUDY AREAS

Glaciated plains

The Glaciated Plains (GP) eco-region encompasses 32% of Missouri and is characterized by rich, productive soils. The GP study area included Andrew, Gentry, DeKalb, and Nodaway counties in northwest Missouri (Figure 1). The combined area of the 4 counties was 5779.29 km^2 and is 2.48% urban areas, 44.50% cultivated crops, 12.26% forest, 37.73% grassland, and 3.03% other. Land enrolled in the Conservation Reserve Program (CRP) made up 19.07% of the grassland vegetation (United States Department of Agriculture [USDA] Farm Service Agency [FSA] 2017). Publicly owned land made up 1.28% of the total area and was mostly comprised of conservation areas owned by the MDC. The most common land uses were farming of cultivated crops, with corn and soybeans totaling 36.98% and 50.86% of all crops grown, respectively, and raising cattle for beef and dairy production. The area was also characterized by low, rolling hills with elevation ranging from 185 m to 475 m, with local relief from 3 m to 30 m (USDA Natural Resources Conservation Service [NRCS] 2006).

The climate consisted of moderately cold winters and warm, humid summers. The mean annual temperature was 11.3° C, with minimum temperatures in January (-8.86° C) and highest temperatures in July (30.52° C; Prism Climate Group, www.prism.oregonstate.edu, accessed 21 Jan. 2018). The average annual precipitation was 94.36 cm, with the lowest precipitation in January (2.1 cm) and the highest in June (13.04 cm; Prism Climate Group).

Land not dominated by agriculture supported grassland vegetation and oak-hickory forest (NRCS USDA 2006). Common grass species included big bluestem (*Andropogon gerardi),* indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium),* switchgrass *(Panicum virgatum),* and wildrye *(Elymus* spp.*).* Upland wooded areas supported southern red oak *(Quercus falcata*), white oak *(Q. alba*), hackberry *(Celtis* spp.*),* shagbark hickory *(Carya ovata*) and bitternut hickory *(C. cordiformis).* Bottomland wooded areas included sycamore *(Platanus occidentalis),* cottonwood *(Populus* spp.), elms *(Ulmus* spp.), green ash *(Fraxinus pennsylvanica*) and silver maple *(Acer saccharinum).*

Based on a study undertaken in the 1990s, fawn pregnancy rates were the highest in the Glaciated Plains at 34%, compared to all other regions in Missouri (Hansen et al. 1996). At the time of this study deer density in the 4 county area was approximately 7 deer/km^2 (K.

Wiskirchen, Missouri Department of Conservation, personal communication). Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) were the two most common predators, with 5 confirmed mountain lion (*Puma concolor*) sightings in the GP since 2006.

Ozarks

The Ozark (OZ) eco-region encompassed 38% of Missouri and was characterized by thin, rocky soils. The OZ study area included Douglas, Howell, Texas, and Wright counties in south-central Missouri (Figure 1). The combined area of the 4 counties was 9,332.25 km^2 and was 2.09% urban areas, 1.69% cultivated crops, 52.65% forest, 42.98% grassland, and 0.59% other. Publicly owned land comprised 14% of the Ozark region and the 4 county area included 600 km^2 of Mark Twain National Forest. The most common land use was the raising of cattle for beef and dairy production, with a total of 3,766 farms with 279,868 head of cattle throughout the four counties (USDA National Agricultural Statistics Service [NASS] 2012). The topography was highly variable, with elevation ranging from 90 m to 500 m and local relief anywhere from 60 m to 240 m (Thom and Wilson 1980, NRCS USDA 2006). Caves, springs, bluffs, and clear-flowing streams were characteristic features of the area.

The climate consisted of moderately cold winters and warm, humid summers. The mean annual temperature was 13.26^{o} C, with minimum temperatures in January (-5.39^{o} C) and high temperatures in August (31.5^{o} C; Prism Climate Group). The average annual precipitation was 115.11 cm, with the lowest precipitation in January (6.63 cm) and the highest in May (12.72 cm; Prism Climate Group).

The OZ was mostly oak-hickory and oak-hickory-pine forests (NRCS USDA 2006). The dominant tree species were black oak (*Quercus velutina*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), post oak (*Q. stellata*), hickory (*Carya* spp.), and shortleaf pine (*Pinus echinata*). Most non-forested areas were created for pasture or hay fields, but some natural glades occurred and supported warm-season grasses, such as big bluestem, indiangrass, and little bluestem.

Based on a study undertaken in the 1990s, fawn pregnancy rates were the lowest in the OZ at 21% (Hansen et al. 1996). At the time of this study, deer density in the 4 county area was approximately 9 deer/km^2 (K. Wiskirchen, personal communication). Coyotes and bobcats were the predominant predators in the area, although a small, recolonizing black bear (*Ursus americanus*) population existed in the southern OZ region. There have been < 45 confirmed mountain lion sightings in the entire OZ region since 2006.

METHODS

Adult White-tailed Deer Capture

We captured yearling (1.5 year old) and adult (>1.5 years old) female deer using modified Clover traps (VerCauteren et al. 1999) and rocket nets (Haulton et al. 2001) from January – March 2015 – 2017. Adult and yearling females were immobilized using Telazol (Tiletamine hydrochloride HCl and zolazepam HCl, 4.4 mg/kg) and xylazine HCl (2.2 mg/kg; Kreeger 1996, Kilpatrick and Spohr 1999) or BAM (Butorphanol Tartrate, Azaperone Tartrate, Medetomidine HCl; Wolfe et al. 2014). We determined pregnancy using a portable trans-abdominal ultrasound (Ibex Lite, E.I. Medical Imaging, Loveland, CO) and inserted a vaginal implant transmitter (VIT; Model M3930 Advanced Telemetry Systems, Inc., Isanti, MN) if the doe was pregnant (Bowman and Jacobson 1998). Captured deer received a uniquely numbered metal ear tag (Hasco Tag Company, Dayton, KY) and were fitted with a 825 g Iridium GPS radio-collar (Model G2110E, Advanced Telemetry Systems) that was programmed to record a location every 5 hours. Collars were equipped with an 8-hour motion sensitive switch that alerted us remotely when the collar remained motionless. We reversed the xylazine HCl with an intravenous injection of tolazoline (4.0 mg/kg; Miller et al. 2004) or reversed the BAM with intramuscular injections of Atipamezole and Naltrexone HCl (Wolfe et al. 2014).

Due to logistical constraints, not all yearling and adult females were chemically immobilized and checked for pregnancy in the field. Therefore, we collected 1 mL – 5 mL of blood to check for pregnancy using pregnancy specific protein B (PSPB) levels (Duquette et al. 2012). All capture and handling procedures were approved by the Institutional Animal Care and Use Committee at the University of Missouri (protocol number 8216).

Neonate Capture

At the beginning of May each year we began monitoring VITs daily and programmed the radio-collars of pregnant females to record a location every hour and upload locations daily at 0600 and 1800. We monitored these locations for movements indicative of parturition, such as significantly reduced daily movements, spending multiple hours in one small area, and repeatedly returning to one particular area (Huegel et al. 1985*a*, Vore and Schmidt 2001, D'Angelo et al. 2004, DeMars et al. 2013). If we suspected that parturition occurred, we searched the area to locate a neonate. If a doe with a VIT had locations that seemed to indicate she had given birth, but the VIT had not been expelled, we waited to search the area until the VIT dropped. When a VIT was expelled we waited 1 – 2 hours before attempting to locate the VIT, to ensure that the female had enough time to bond and imprint with neonate(s) to reduce the risk of abandonment (Chitwood et al. 2015*b*). We also captured neonates opportunistically by grid searching likely fawning cover and through the use of landowner reports.

When a neonate was located we put on nitrile gloves to reduce the amount of scent transferred to the neonate (Livezey 1990), then blindfolded, sexed, and weighed the neonate to the nearest 0.01 kg. All neonates were fitted with an expandable breakaway 68 g VHF radio-collar (Model M4210, Advanced Telemetry Systems Inc.) that was equipped with a motion sensitive mortality switch on a 4 hour delay. We measured the new hoof growth, recorded hoof and umbilicus characteristics and noted behavior during capture; we used these metrics to estimate an age at capture for neonates that were not found with a VIT (Sams et al. 1996, Brinkman et al. 2004). We calculated the birth date by subtracting the estimated age from the capture date. For neonates caught using a VIT that was expelled at an identifiable birth site, date of birth was the date the VIT was expelled (Bishop et al. 2011, Hasapes and Comer 2017).

We monitored neonates for survival once per day for the first 30 days of life, every other day for the following 30 days, and then 1 – 2 times per week until the deer died or the collar fell off. When a mortality signal was heard we tried to reach the carcass as quickly as possible to conduct a field necropsy, but given constraints with land access we were not always able to investigate the mortality that same day. Therefore, scavenging likely occurred before we reached the carcass so we did not assign cause of death as predation unless we found conclusive evidence of predation, such as killing bite marks in the head or neck (White 1973). Neonates are the age class most susceptible to predation (Ballard 2011) so if we were unable to find the head, but found other evidence that a predator was present and killed the neonate (i.e. cached; O’Gara 1978, Labisky and Boulay 1998) we classified the mortality as possible predation (Kilgo et al. 2012). Bobcats, coyotes, and black bears were present in our study areas, so we used characteristics associated with their killing from the literature (O’Gara 1978, Mathews and Porter 1988, Labisky and Boulay 1998) to assign a possible predator.

If the carcass was found intact with no signs of scavenging or predation, we collected the carcass and sent it to MDC to be necropsied by the state wildlife veterinarian. If the cause of death was starvation we assumed that it was abandoned. Some studies have omitted abandoned fawns from their analysis because it was thought to be marking induced (Nelson and Woolf 1987, Livezey 1990); however, other studies have found little evidence of this to be true (Vreeland et al. 2004, Powell et al. 2005). Since maternal abandonment is a natural form of mortality for neonates, removing these mortalities from the survival analysis would overestimate neonate survival (Powell et al. 2005). Therefore, we included abandoned neonates in our survival analysis.

Home Range Estimation

To determine how neonate survival to 8 weeks was affected by changes in land use by the dam over time we calculated home ranges weekly for all does with a radio-collared neonate. We began creating these weekly home ranges on the day the neonate died and worked backwards until the estimated day of birth. Does alter their movements following the death of their neonate (Bartush and Lewis 1978, DeMars et al. 2013), so this approach ensured that we did not incorrectly estimate doe space use by including locations following a neonate mortality. If a neonate lived all 8 weeks, then we started calculating home ranges on the estimated day of parturition and ended 8 weeks later. We calculated home ranges using the dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012).

The dBBMM computes home ranges by creating a utilization distribution (UD; Worton 1989) that incorporates both the size of the area of use and the animal's intensity of use within this area. The dBBMM creates a UD by modeling the space use between 2 continuous locations as Brownian movement, a continuous random walk in which movement is diffusive and equally likely in any direction (Turchin 1998, Horne et al. 2007). The dBBMM requires the fixed position, time of each location, error associated with the locations (GPS collar error), and the degree to which movement between locations deviates from a straight line, also known as the magnitude of variance of the Brownian motion (σ_m^2). To account for behaviorally distinct movements that change over time, the dBBMM allows σ_m^2 to vary along the movement path (Gurarie et al. 2009, Kranstauber et al. 2012) using an adjusted version of the behavioral change point analysis (Gurarie et al. 2009) via a sliding window with *w* locations along a path. The window moves along the movement path and calculates a new σ_m^2 for each step every time it falls within the window. These σ_m^2 estimates are averaged to get a final σ_m^2estimate for each step.

Choosing the size of the window is a critical step because a tradeoff exists between the greater reliability in the estimation of σ_m^2 with a large window size and the short term changes that can be detected with a small window. Also, a margin (*m*) greater than 3 locations is needed on either end of the window in which no break points can occur. We used a window size of 7 (equivalent to 7 hours) and a margin of 3 that we chose based on the cross-validation techniques suggested by Kranstauber et al. (2012). We used a GPS collar error of 5.92 m that we determined by performing GPS collar accuracy field tests (Appendix A) and used the move package (Kranstauber et al. 2017) in Program R version 3.4.3 (R Core Team 2017) to calculate home ranges.

Survival modeling

We estimated 8 and 16-week survival rates in each study area using the Kaplan-Meier (KM) estimator to use as a baseline comparison of survival in each study area (Pollock et al. 1989). We then used the Andersen-Gill (AG) formulation of the Cox proportional hazards (CPH) model with an age-based time scale (Fieberg and DelGiudice 2009) to estimate the effects of habitat on the survival of neonatal white-tailed deer (Andersen and Gill 1982, Duquette et al. 2014). The CPH model is well suited to handle the range and variability of hazards found in wildlife populations because it does not assume a specific hazard function (Murray 2006).

The AG model is a derivation of the CPH model as a counting process and can accommodate left and right censored data, time-dependent covariates, multiple events and discontinuous intervals of risk (Therneau and Grambsch 2000, Johnson et al. 2004). The AG model computes a hazard ratio (HR), which compares hazards between covariates and estimates the effect of covariates on the baseline hazard rate. A hazard ratio of 1 indicates there is no effect of the covariate on the risk of mortality, whereas a HR of <1 or >1 indicates a decreasing or increasing mortality risk, respectively. The HR is calculated by taking the natural exponent of the β estimate calculated by the model.

The assumptions of the AG model are that censoring is independent of survival, individual fates are mutually independent, covariates vary linearly with the log hazard and that hazard ratios between individuals are proportional and remain constant over time. We tested the proportional hazards assumption by plotting the scaled Schoenfeld residuals for each variable against time (Grambsch and Therneau 1994, Johnson 2004). We tested all models, but only report the tests if we saw a significant violation of the assumption. If the models violated the assumption, we transformed the offending covariate into a time dependent coefficient using the time transform functionality of coxph (Therneau et al. 2017).

Model development

We constructed 2 sets of candidate AG survival models for each study area: model set 1 quantified the influence of biological covariates on neonate survival (Table 1) and model set 2 quantified the influence of habitat covariates (Table 2) within the dams' weekly home range on neonate survival (Table 3; Rohm et al. 2007, Grovenburg et al. 2011, 2012*a*, Jacques et al. 2015). Biological variables included capture year, sex, birth mass, and birth date, all of which have been important in understanding neonatal deer survival in other regions (Rohm et al. 2007, McCoy et al. 2013). The effect of sibling status on neonate survival is unclear (Bishop et al. 2008, Chitwood et al. 2015*b*), and we were not certain that we correctly determined sibling status for every neonate, so we did not include this as a covariate. We estimated birth mass by regressing neonate mass at capture (nearest 0.01 kg) on age at capture separately for each study area and sex, and used the estimated regression coefficients to predict birth mass (Smith et al. 1997, Eacker et al 2016). We used the best approximating model from model set 1 as the underlying structure for all models in model set 2 (Burnham and Anderson 2002, Hill et al. 2003, Zablan et al. 2003, Rohm et al. 2007).

To obtain the habitat covariates used in model set 2 we downloaded the 2011 land cover layer from the National Land Cover Database (NLCD; Homer et al. 2015) and reclassified the 15 land cover types into the main land cover types found throughout the study areas: forest, grassland, crop, CRP (in the GP only), and other. In the GP, grassland areas enrolled in the conservation reserve program (CRP) comprise 19.07% of the grassland vegetation (USDA NASS 2017). CRP grasslands can influence neonate survival (Grovenburg et al. 2012*a*), so we obtained a CRP raster layer from the USDA NRCS and merged it with the land cover layer obtained from the NLCD. CRP only comprises 1.8% of the grassland vegetation in the OZ, so we did not include this land use type in the OZ. We cropped the re-classified land use layer to each weekly doe home range and used FRAGSTATS version 4.2 (McGarigal et al. 2012) to compute metrics (Table 2) that described the habitat in each home range. We selected these habitat variables based on neonate ecology and other studies (Vreeland et al. 2004, Rohm et al. 2007, Grovenburg et al. 2011, 2012*a*, Gulsby et al. 2017).

We considered resource availability (Duquette et al. 2014) and the ability of predators to locate neonates (Rohm et al. 2007) as the two main factors influencing neonate mortality, so we combined the habitat variables in Table 2 so they represented these predictions (Table 3). To describe resource availability we used landscape scale metrics that described the home range as a whole and characterized the diversity of habitat types, size of the home range, and amount of edge within the home range. We predicted that as these metrics increased, resource availability would increase and neonate survival would increase (Duquette et al. 2014).

We used mainly class scale metrics, or metrics that described the amount and spatial configuration of one habitat type (McGarigal et al. 2012), to investigate the influence of predators on neonate survival. These class scale metrics included amount of cover and non-cover habitat, and the mean patch shape and size of each habitat type (Table 3, Rohm et al. 2007). We considered forest to be a cover habitat, crop as non-cover habitat, and grassland as both given our inability to determine whether those areas were pasture (non-cover) or tall hay fields (cover; Grovenburg et al. 2012*a*, *b*). We considered CRP grasslands in the GP to be cover habitat (Grovenburg et al. 2012*a*, *b*). We defined crop habitat as non-cover because by the end of May about 85% of all corn crops and 20% of all soybean crops have emerged, but are not likely to be tall enough to offer substantial cover to neonates (Grovenburg et al. 2012*a*, USDA 2017).

We tested for collinearity of independent habitat variables and did not include covariates with a correlation coefficient $|r| \geq 0.7$ in the same model together (White et al. 2010). In the OZ few does had crop within their home ranges so we did not include crop metrics in the OZ survival models. We ran all models using the package survival (Therneau 2017) in Program R. We used the R package simPH (Gandrud et al. 2015) to simulate the effects of each important predictor on relative hazards across their range of observed values, and used the function simGG to plot these results.

We used Akaike's Information Criterion scores corrected for small sample size (AIC_c) to determine the best model in the candidate set and considered models within 2 ΔAIC_c units as competing for the top model (Burnham and Anderson 2002). If models within this threshold only differed from the top model only by one additional parameter we considered that parameter to be uninformative and unsupported by the data. If other models were within 5 ΔAIC_c and had 95% confidence intervals of beta parameters that did not include 0 we estimated coefficients using model averaging (Burnham and Anderson 2002). We calculated the model averaged parameter estimates, unconditional standard errors, and unconditional confidence intervals for all parameters included in models within 5 ΔAIC_c from the most supported model (Burnham and Anderson 2002, pgs 169 – 170). We examined the relative importance of individual parameters by summing the Akaike weights across all models that contained the parameter of interest. We conducted model selection and model averaging using the package AICcmodavg (Mazerolle 2017) in Program R.

RESULTS

Capture, cumulative survival and cause-specific mortality

During 2015 – 2017 we captured and collared 186 female fawn (6-month old), yearling, and adult deer (2015: 30 GP, 37 OZ; 2016: 30 GP, 39 OZ; 2017: 24 GP, 26 OZ), and placed VITs in 82 females that lived until parturition (2015: 3 GP, 7 OZ; 2016: 18 GP, 19 OZ; 2017: 19 GP, 16 OZ). We successfully caught ≥ 1 neonate for 64 out of 82 VITs (78%) and caught a total of 226 neonates from 2015 – 2017 (Table 4). We removed one opportunistically captured neonate in the GP from the analysis because it was thought to be > 2 weeks of age and we did not want to incorrectly estimate its birth date and birth mass. Of the remaining neonates, 183 (GP: 85, OZ: 98) came from 111 collared mothers that had enough locations to create at least 1 post parturition home range. Mean age at capture was 2.96 ± 3.1 (SD) days in 2015, 0.81 ± 1.11 days in 2016, and 0.88 ± 1.13 days in 2017.

Peak birth dates in the GP were 27 May 2015, 29 May 2016, and 28 May 2017, and the earliest dates of birth were 12 May 2015, 20 May 2016, and 12 May 2017. The average estimated birth mass in the GP in 2015 was 3.07 ± 0.51 kg (SD), 3.38 ± 0.69 kg in 2016, and 3.49 ± 0.67 kg in 2017. In the GP the 8 and 16-week KM survival estimates were 0.43 (95% CI = 0.35 – 0.54) and 0.42 (95% CI = 0.33 – 0.52), respectively (Figure 2).

Of the 63 deaths observed in the GP we attributed 14 to predation, 5 to natural causes other than predation, 3 to other, and 41 to unknown. We attributed 2 predation mortalities to coyotes and 1 to bobcats, with the rest identified as either bobcat or coyote because of lack of conclusive evidence indicating either predator. Of the unknown mortalities, 3 were categorized as likely predation. Observed causes of natural mortalities were abandonment and starvation (n=2), drowning (n=2), and unknown illness (n=1). The other category included being hit by a hay combine (n=2) and vehicle collision (n=1).

Peak birth dates in the OZ were 23 May 2015, 29 May 2016, and 23 May 2017, and the earliest dates of birth were 15 May 2015, 9 May 2016, and 12 May 2017. In the OZ the average estimated birth mass in 2015 was 2.63 ± 0.56 kg (SD), 2.94 ± 0.60 kg in 2016, and 2.74 ± 0.60 kg in 2017. In the OZ the 8 and 16-week KM survival estimates were 0.47 (95% CI = 0.38 – 0.57) and 0.44 (95% CI = 0.35 – 0.54), respectively (Figure 2).

Of the 62 deaths observed in the OZ we identified 16 as predation, 4 as natural causes other than predation, 3 as other, and 39 as unknown. Of the 16 predation mortalities, 3 were bobcat kills, and 1 was a coyote, with the rest identified as either bobcat or coyote due to lack of conclusive evidence indicating either predator. The 4 natural causes were abandonment (n = 3), and drowning (n = 1). The other category included being hit by a hay combine (n = 2), and vehicle collision (n = 1). The unknown category included 3 possible predations by either coyote or bobcat. We did not find black bear sign at any mortality site, but it is possible that they killed neonates in the OZ.

Survival modeling

Glaciated Plains. – We identified 7 plausible intrinsic survival models (within 2 ΔAIC_c) that explained neonate survival (Table 5). The top supported model indicated that sex and year were important for neonate survival. However the 95% confidence intervals of β estimates for the parameters sex (β = 0.48, 95% CI = -0.04 – 0.99) and year (2016: β = 0.72, 95% CI = -0.01 – 1.45; 2017: β = 0.53, 95% CI = -0.21 – 1.28) overlapped 0, so we considered this model to be uninformative. The second best model indicated that sex best explained neonate survival, but the 95% confidence interval of the β estimate for sex (β = 0.44, 95% CI = -0.07 – 0.99) also included 0 so we considered this model to be uninformative. The third best model (ω = 0.09) was the null model, and all models ranked lower than the null model had 95% confidence intervals of β estimates that included 0. Thus we considered the null model to be the best model in this model set, and carried the null model forward to model set 2 containing the landscape scale parameters for the GP.

In model set 2 we determined that models containing mean forest patch size violated the proportional hazards assumption. Therefore, we included the mean forest patch size covariate and a log time interaction for the covariate in each model that violated the assumption (Therneau et al. 2017). We identified 3 models within 2 ΔAIC_c from the top model and 10 additional models within 5 ΔAIC_c from the top model (Table 6); thus, we used model averaging to determine parameter estimates (Burnham and Anderson 2002; Table 7). According to model averaging the best explanatory covariates were landscape shape index (LSI), mean shape index, and mean forest patch size and its log time interaction (Table 7). Observed LSI values ranged from 1.23 –5.78, with a mean of 2.82; a LSI value close to 1 indicated that the home range consisted of 1 square of 1 land cover type, with larger values indicating more disaggregated patch types and more edge. Increasing LSI by one unit and holding all other covariates constant, increased the mortality risk by 1.6 times (Hazard Ratio [HR] 95% CI = 1.12 – 2.29; Figure 3a). Observed mean shape index values ranged from 1.07 – 2.63, with a mean of 1.67; shape values of 1 indicated all patches within the home range were square shaped, and as the shape index value increased, the complexity of the shape increased. An increase in mean shape index by 1 unit, increased a neonate's mortality risk by 2.94 times (HR 95% CI = 1.22 – 7.17; Figure 3b).

The effect of mean forest patch size on neonate survival changed over time, as indicated with the violation of the proportional hazards assumption. At birth, increasing mean forest patch size by 1 ha increased mortality risk by 1.28 times (HR 95% CI = 1.04 – 1.57; $\beta = 0.25$); as neonates aged mortality risk due to mean forest patch size decreased in relation to the function $\beta(t) = 0.25 - 0.09 \times \log(t)$ (Therneau et al. 2017; Table 7). By the time neonates were about 2 weeks old average forest patch size did not affect survival, and after this time increases in forest patch size slightly decreased their mortality hazard (Figure 3c).

Ozarks. – Sex × birth mass was the most supported model for the Ozarks (Table 5). The next best model was 9.00 ΔAIC_c away; we thus included sex × birth mass in every model in candidate set 2 for the OZ region. The top model indicated that birth mass significantly impacted female neonate survival (birth mass: $\beta = -2.17$, 95% CI = -3.38 – -0.96, sex × birth mass: $\beta = 2.03$, 95% CI = 0.73 – 3.33, sex: $\beta = -4.69$, 95% CI = -7.92 – -1.50); when females were born at a low birth mass (i.e., lower than the first quartile of observed birth masses) their survival was lower than males, but if they were born with a birth mass greater than the mean observed birth mass female survival was greater than males (Figure 4).

In model set 2 we determined that models containing the grassland patch density covariate violated the proportional hazards assumption. Therefore, we included the grassland patch density covariate and a log time interaction for the covariate in each model that violated the assumption (Therneau et al. 2017). Following Therneau et al. (2017), we determined that $\beta(t) = ax + xlog(t + 5)$ fit the data better than $\beta(t) = ax + xlog(t)$, so we used the first structural form in our models. Due to model selection uncertainty in model set 2 (Table 6), we used model averaging to determine parameter estimates (Table 7). The most supported covariates were percent grassland, and grassland patch density and its log time interaction (Table 7). Increasing the percentage of grassland within a home range by 1% and holding all other covariates constant, decreased the mortality risk by 2% (HR 95% CI = 0.96 – 0.99; Figure 5a). The effect of grassland patch density on neonate survival decreased over time, as indicated with the violation of the proportional hazards assumption. At birth, increasing grassland patch density by 1 patch per 100 hectares increased mortality risk by 1.23 times (HR 95% CI = 1.08 – 1.43; $\beta = 0.20$); as neonates aged the mortality risk due to grassland patch density decreased in relation to the function $\beta(t) = 0.21 - 0.08 \times \log(t + 5)$ (Therneau et al. 2017; Table 7). By the time neonates were about 2 weeks old, grassland patch density had no effect on neonate survival (Figure 5b).

DISCUSSION

Despite differences in predator species, land use, habitat types, and levels of fragmentation the 8 and 16-week survival estimates were similar in the OZ and GP. This similarity in survival rates is in contrast with other neonate survival studies conducted in 2 disparate regions, which observed decreased neonate survival in areas with higher predator densities, worse habitat quality, or both (Vreeland et al. 2004, Shallow et al. 2015, Warbington et al. 2017). However we had no *a priori* beliefs that either study area was better than the other in terms of forage quality, cover habitat, or lower predator densities; therefore, it seems reasonable that neonate survival was similar in both regions.

Despite similarities in survival estimates, we found different underlying factors influencing neonate survival in the two regions. In the GP we found no evidence of any intrinsic factors contributing to higher mortality, but in the OZ we found that low birth mass significantly reduced female neonate survival. Differences in mean birth masses between the two areas likely led to this difference; in the GP neonates had a greater mean birth mass than neonates in the OZ by 0.44 kg – 0.75 kg each year, and the lowest birth mass observed in the GP was 0.43 kg greater than the lowest observed birth mass in the OZ. Neonate ungulate birth mass is often directly related to maternal body mass and condition (Verme 1969, Cook et al. 2004, Michel et al. 2015, Long et al. 2016), though other factors such as litter size, maternal age, and maternal social rank can also influence birth mass (Robinette et al. 1973, Michel et al. 2015). Deer in the GP are larger bodied than deer in the OZ, which likely led to heavier neonate birth masses in the GP (Steiger 2013, Michel et al. 2015). Neonates born at greater birth masses often have increased growth rates compared to lighter neonates (Verme 1989, Steiger 2013). Faster growing neonates can escape predators earlier, thus increasing their survival probability (Nelson and Woolf 1987, Kunkel and Mech 1994, Lomas and Bender 2007). Further, if neonates have low mass at birth (i.e., < 1.9 kg), they might be unviable at birth and unlikely to live longer than 24 hours regardless of predators (Verme 1962, 1963, Lomas and Bender 2007).

It is interesting that we only observed this relationship of low birth mass leading to higher mortality in female neonates but not in males. Male white-tailed deer neonates are hypothesized to grow at a faster rate than females (Hewison and Gaillard 1999); therefore, males might be able to overcome the limitations imposed by a low birth mass at an earlier age than females, which would increase their survival probability. However, when neonates were born above mean birth mass values, males had higher mortality rates than females (Figure 4). Other neonate survival studies have found that males had lower survival rates than females because of differences in activity patterns between the sexes (Aanes and Anderson 1996, Raedeke et al. 2002). Males are theorized to be more active than females (Jackson et al. 1972, Aanes and Anderson 1996), and spend more time away from the dam (Taber and Dasmann 1954), which would increase their probability of being depredated. It is possible that when born at low birth masses female neonates are more susceptible to predation because they are not growing as fast as males, but when born at average birth masses males are more susceptible to predation because of their higher activity rates.

Determining accurate cause-specific mortality in neonate survival studies is difficult and time consuming because it involves intensive mortality checks (≤ every 8 hours in some studies), the ability to reach carcasses quickly, and DNA evidence of specific predators (Kilgo et al. 2012, Chitwood et al. 2015*b*, Shuman et al. 2017). As a result, determining cause-specific mortality was not an objective in this study and the majority (63 – 65%) of our mortalities was classified as unknown. We were conservative in assigning a cause of death because we did not want to overestimate the influence of any one mortality source on neonate survival. Furthermore, many of our mortality investigations occurred after scavengers had been present, thus making conclusions about cause of death even more difficult. Given results from studies in similar regions, it is likely that predators were the leading cause of mortality (Huegel et al. 1985*b*, Rohm et al. 2007, Grovenburg et al. 2011, Warbington et al. 2017), even though we could not definitively conclude this from our data. Both study areas had populations of coyotes and bobcats, but we did not have estimates of abundance in either region, and it is possible that predator densities were not uniform between the OZ and GP.

In the OZ there is a small, recolonizing population of black bears which does not exist in the GP (Wilton et al. 2014). Black bears can be a significant source of predation for neonates, particularly in the first few weeks of life (Kunkel and Mech 1994, Carstensen et al. 2009, Shuman et al. 2017). However, bear density in the OZ was approximately 0.02 bears/km^2 (Wilton et al. 2014), which is a lower density compared to regions where bears are a significant mortality source (e.g., 0.66 bears/km^2 – Shuman et al. 2017, 0.16 – 0.20 bears/km^2 – Carstensen et al. 2009). Also, Ballard (1992) found that black bears were only a substantial cause of moose (*Alces alces*) calf mortality when they occurred at densities > 0.20 bears/km^2. Therefore, it is unlikely that black bears caused a significant amount of neonate mortality in the OZ during this study. However, as the black bear population continues to expand and grow it is possible that black bears will cause more neonate mortalities and potentially reduce neonate survival in the OZ (Ballard 1992, Shuman et al. 2017).

White-tailed deer are thought to prefer edge habitats because of the high diversity of browse and forbs within these habitats (Stewart et al. 2011), which can provide high quality nutritional forage for dams during gestation and lactation (Rohm et al. 2007). However, Gates and Gysel (1978) proposed that predators view edges as better foraging opportunities because these areas tend to harbor greater prey densities, which would negatively impact neonates. Furthermore, hard edges, or edges between habitats with differing habitat heights, have been linked to higher predation rates (Schneider et al. 2012). In the GP we observed that greater amounts of edge and more complex edges within the dams' home range resulted in decreased neonate survival, which is in contrast with other studies (Rohm et al. 2007, Van Moorter et al. 2009, Jacques et al. 2015, Gulsby et al. 2017) and in the OZ we found no relationship between edge and neonate survival. Edges in the OZ were between hayfields, grassland, and forests, and tended be soft edges. In the GP, edges between emerging corn and soybean fields dominated the landscape, and thus were hard edges at the time of parturition (Schneider et al. 2012, USDA NASS 2017). Edges in both study areas likely provided increased nutritional forage for dams compared to interior habitats, but the abundance of hard edges in the GP could have increased predation on neonates, thus reducing their survival.

We observed that the density of grassland patches in the OZ and size of forest patches in the GP decreased survival, but only until neonates were about 2 weeks old. Neonatal fawns are 'hiders' for the first few weeks of life; they bed down and remain inactive while the dam is away foraging to reduce their risk of predation (Lent 1974, DeYoung and Miller 2011). This time period is often marked by high predation because neonates are unable to flee from predators (Rohm et al. 2007, Grovenburg et al. 2011, Chitwood et al. 2015*b*, Shuman et al. 2017), but by 2 weeks old neonates are thought to be mobile enough to outrun some predators (Rohm et al. 2007, Grovenburg et al. 2011). Given the timing of when patch size and density stopped affecting neonate survival, it is possible that these metrics are related to predator searching efficiency (Andrén and Angelstam 1988, Brown and Livatitis 1995, Rohm et al. 2007). The smaller, more fragmented patches of grassland in the OZ might have been easier for predators to search thoroughly, resulting in higher neonate mortality in these patches. Other studies (Rohm et al. 2007, Grovenburg et al. 2012, Gulsby et al. 2017) have also found a similar relationship between small habitat patches and neonate survival. However, in the GP we found the opposite in which large forest patches led to decreased survival. This opposite relationship could be related to the high degree of forest fragmentation in the GP; the maximum average forest patch size observed in the GP was 14.14 ha, which was 10.23 times smaller than the maximum average forest patch size observed in the OZ, and 3.93 times smaller than the maximum average grassland patch size in the OZ. It is possible that large forest patches in the GP were still small enough for predators to search efficiently, which would result in higher neonate mortality in these patches. Small patches of forest (i.e. < 1.16 ha) were generally fencerows between crops which tended to be unmanaged with a very thick understory. These small patches of forest could have reduced a predator's ability to locate neonates because of the dense understory, thus increasing neonate survival in small patches of forest until they were 2 weeks of age (Richer et al. 2002).

We reached several different conclusions about how and when habitat metrics affected neonate survival compared to other studies. This difference is in part likely due to the many differences in habitat, predator densities, and land use between regions, and the complexity of neonate survival. However, one large difference in our study was our use of the dams' weekly home range as the base from which to calculate our habitat metrics. Dams and neonates shift their space use (DeYoung and Miller 2011) and alter their resource selection (Long et al. 2009, Van Moorter et al. 2009) as neonates age. Therefore, we would expect that the habitat influencing neonate survival would change in space and time, and would not be accurately reflected by a circular buffer of the capture location. By creating different home ranges on a weekly basis we were able to directly compare the landscape features experienced by a neonate that lived during a specific week of life to those experienced by a neonate who died during that same week, thus potentially making more accurate comparisons. Further, we did not extrapolate our home ranges to include habitats that a neonate might have experienced had it lived long enough to do so; we only included locations for dam home ranges up until the day the neonate died and no further. We recognize that the use of the dams' home range might not be a completely accurate depiction of neonate space use, so we recommend that neonate GPS collars be used in the future to determine how neonate space use changes over time and affects survival.

MANAGEMENT IMPLICATIONS

Neonate survival was impacted by large scale habitat characteristics in a way that was seemingly dependent on the broader context of the landscape. In the OZ, where the landscape was more uniform and less fragmented, survival was related only to class scale metrics, or metrics that described the amount and spatial distribution of one habitat type surrounding the neonate (McGarigal et al. 2012). In contrast, in the GP where the landscape was more diverse and habitat patches were highly fragmented, neonate survival was also affected by landscape scale habitat metrics, or metrics that described the spatial pattern of the area surrounding the neonate (McGarigal et al. 2012). Perhaps in more fragmented and diverse areas, where different habitat patches are well interspersed, the spatial configuration of the landscape affects neonate survival more than the amount of any specific habitat type. Neonate survival is a complex process that involves habitat metrics at multiple spatial scales, from localized bed sites to the broader landscape in which the neonate resides; thus, managers should consider not just increasing amounts of habitats that are theorized to have the best cover for neonates or forage quality for dams, but also realize that the configuration of all habitats might affect survival in a complex and fragmented landscape. Therefore, in more fragmented areas we recommend that managers try to maintain large (i.e., > 14 ha) contiguous patches of forested habitat or grasslands, thus reducing the total amount of edge habitat in the landscape. We also recommend that managers try to maintain edges as gradual transitions between disparate habitat types.

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TABLES

Table 1. Set of candidate models created for model set 1 to determine the influence of intrinsic factors on neonatal white-tailed deer survival in the Ozark and Glaciated Plains regions of Missouri, USA, 2015 – 2017.

Model	**K**[a]	**Description**
S_{Constant}	0	Survival is constant
S_{Sex}	1	Survival varies by the sex of the fawn
S_{Year}	2	Survival varies among the 2 capture years
S_{Mass}	1	Survival varies by the birth mass
$S_{\text{Date of birth}}$	1	Survival varies by Julian date of birth
$S_{\text{mass +date of birth}}$	2	Survival varies by mass and date of birth
$S_{\text{year + mass}}$	3	Survival varies by year and birth mass
$S_{\text{year + Date of birth}}$	3	Survival varies by year and date of birth
$S_{\text{year} \times \text{mass}}$	5	Survival varies differently by year and birth mass
$S_{\text{sex + mass}}$	2	Survival varies by sex and birth mass
$S_{\text{sex}\times\text{mass}}$	3	Survival varies differently by sex and birth mass
$S_{\text{date of birth} \times \text{mass}}$	3	Survival varies differently by date of birth and birth mass
$S_{\text{date of birth} \times \text{year}}$	5	Survival varies differently between year and date of birth
$S_{\text{year} \times \text{sex}}$	5	Survival varies differently between year and sex
$S_{\text{Sex + year}}$	3	Survival varies by year and sex
$S_{\text{sex + date of birth}}$	2	Survival varies by sex and date of birth
$S_{\text{year + mass + sex}}$	4	Survival varies by year, mass and sex
$S_{\text{year + mass + date of birth}}$	4	Survival varies by year, mass and date of birth
S_{global}	13	All parameters

[a] Number of parameters.

Table 2. Final set of variables we measured within weekly post-parturition dam home ranges to model the influence of habitat characteristics on neonate white-tailed deer survival in the Ozark and Glaciated Plains regions of Missouri, USA, 2015 – 2017.

Metric type	Variable	Number	Definition[a]
Landscape scale metrics	Landscape shape index	1	A standardized measure of total edge or edge density that adjusts for the size of the landscape.
	Contagion	2	Measures the degree to which patch types are aggregated or clumped together.
	Shannon's diversity index	3	Measures the proportional diversity of patches on the landscape.
	Mean shape index	4	Measures the shape complexity of all the patches within the landscape.
Patch scale metrics	Forest patch density	5	Density of forest patches.
	Mean forest patch size	6	Average forest patch size
	Crop patch density	7	Density (no/100ha) of cropland patches
	Mean crop patch size	8	Average crop patch size
	Grassland patch density	9	Density (no/100ha) of grassland patches
	Mean grassland patch size	10	Average grassland patch size
	CRP[b] patch density	11	Density (no/100ha) of CRP patches

Mean CRP patch size	12	Average CRP patch size
Percent forest	13	Total forest cover (%)
Percent crop	14	Total crop cover (%)
Percent grassland	15	Total grassland cover (%)
Percent CRP	16	Total CRP cover (%)
Doe home range size	17	Size (ha) of does weekly home range

[a] See McGarigal et al. 2012 for a more complete definition

[b] Conservation Reserve Program grasses. This land cover type is only found in the Glaciated Plains study area

Table 3. Set of candidate models included in model set 2 used to determine the influence of habitat variables within weekly dam home ranges on neonate white-tailed deer survival in the Ozark and Glaciated Plains regions of Missouri, USA, 2015 – 2017.

Hypothesis	Model[a]	Variables[b]
Resource availability	Landscape shape index + shannon's diversity index	1, 3
	Home range + shannon's diversity index	3,17
	Shannon's diversity index	3
	Landscape shape index	1
	Mean shape index	2
Predation – cover habitats	Percent forest	13
	Percent CRP	16
	Percent forest + forest patch density	5, 13
	Percent CRP + CRP patch density	11,16
Predation – non-cover habitats	Home range + percent crop	14, 17
	Percent crop	14
	Percent crop + crop patch density	7, 14
Predation – cover and non-cover habitats	Forest patch density + grassland patch density + CRP patch density + crop patch density	5, 7, 9, 11
	Percent forest + percent crop	13, 14
	Forest patch size + crop patch size	6, 8

	Percent CRP + percent crop	14, 16
	Percent grassland + percent crop	14, 15
	Percent grassland	15
	Forest patch size + grassland patch size + CRP patch size	6, 10, 12
	Forest patch density + grassland patch density + CRP patch density	5, 9, 11
	Percent grassland + grassland patch density	9, 15
Predation – landscape and patch configuration	Home range	17
	Contagion	2
	Contagion + home range	2, 17
	Grassland patch size + mean shape index	4, 10
	Forest patch size + mean shape index	4, 6
	CRP patch size + mean shape index	4, 12
	Crop patch size + mean shape index	4, 8
	Landscape shape index	1

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[a] CRP = grasses enrolled in the Conservation Reserve Program, only found in the GP study area. Crop = row crop agriculture, only found in the GP study area. Grasslands are included in the combine cover and non-cover hypotheses because we were not able to distinguish between pasture (non-cover) and hay fields (cover).

[b] See description in table 1

Table 4. Summary of neonatal white-tailed deer capture results by year, study area, capture method, and sex in the Glaciated Plains and Ozark ecoregions of Missouri, USA 2015 – 2017.

Study Area	Capture Method	2015	2016	2017
Glaciated Plains	VIT	5	19	22
	Collared Doe	10	17	16
	Opportunistic	14	6	3
	Male	16	24	21
	Female	13	18	20
Ozarks	VIT	8	20	15
	Collared Doe	12	20	24
	Opportunistic	7	4	4
	Male	11	28	32
	Female	16	16	11

Table 5. Top biological survival models, ranked according to Akaike's Information Criterion scores corrected for small sample size (AIC_c) and model weights (ω_i), for white-tailed deer fawns in the Glaciated Plains and Ozark regions of Missouri, USA 2015-2017.

Study Area	Model[a]	K[b]	AICc	ΔAICc	ω_i
Glaciated Plains	Sex+Year	3	525.97	0.00	0.15
	Sex	1	526.05	0.08	0.15
	Null	0	527.01	1.04	0.09
	Sex+Mass	2	527.27	1.30	0.08
	Year	2	527.29	1.32	0.08
	Mass	1	527.61	1.64	0.07
	Sex+DOB	2	527.77	1.80	0.06
	Sex+Year+Mass	4	527.84	1.87	0.04
	DOB	1	528.52	2.55	0.04
	Mass+Year	3	528.73	2.76	0.04
Ozarks	Sex×Mass	3	494.77	0.00	0.96
	Sex+Mass	2	503.77	9.00	0.01
	Mass	1	504.61	9.85	0.01
	Global	13	506.05	11.29	0.00

[a] DOB = Julian date of birth, Mass = estimated birth mass.

[b] Number of parameters estimated in each model.

Table 6. Top Andersen-Gill proportional hazards models used to determine the influence of habitat variables within the dams' home range on white-tailed deer neonate survival in the Glaciated Plains and Ozark regions of Missouri, USA 2015 – 2017. They are ranked according to Akaike's Information Criterion scores corrected for small sample size (AIC_c) and model weights (ω_i). We only report models that were < 5 ΔAICc from the top model.

Study Area	Model[a]	K[b]	AICc	ΔAICc	ω_i
Glaciated Plains	Landscape shape index	1	405.10	0.00	0.23
	Landscape shape index + SHDI	2	406.49	1.39	0.11
	Mean forest patch size + mean shape index	3	406.50	1.40	0.11
	Mean shape index	1	407.14	2.04	0.08
	Home range size + SHDI	2	407.38	2.28	0.07
	Contagion + Home range size	2	407.47	2.37	0.07
	SHDI	1	408.46	3.36	0.04
	Mean grassland patch size + mean shape index	2	408.59	3.49	0.04
	Mean CRP patch size + mean shape index	2	408.80	3.70	0.04
	Home range size	1	408.81	3.71	0.04
	Percent grassland + grassland patch density	2	408.84	3.74	0.03
	Mean crop patch size + mean shape index	2	409.16	4.06	0.03
	Contagion	1	409.72	4.63	0.02
Ozarks[c]	Percent grassland + grassland patch density	6	415.27	0.00	0.76
	Percent grassland	4	419.92	4.65	0.07

[a] SHDI = Shannon's diversity index, CRP = Grasslands enrolled in the Conservation Reserve Program

[b] Number of parameters estimated in each model.

[c] All models in the Ozarks contain sex x mass, the top model from the intrinsic set of candidate models

Table 7. Model averaged coefficients, standard errors, and 95% confidence intervals for Andersen-Gill proportional hazard models, representing the effects of habitat covariates within a dams' post-parturition home range on neonatal white-tailed deer survival for the first 8 weeks of life in Missouri, USA, 2015 – 2017. We report the relative variable importance as the sum of Akaike weights (ω_i) across all the models in the set where the variable occurs.

				95% CI			HR[b] 95% CI		
Study Area	Parameter[a]	Estimate	SE	Lower	Upper	HR[b]	Lower	Upper	ω_i
Glaciated Plains	Landscape shape index	0.47	0.18	0.11	0.83	1.60	1.12	2.29	0.34
	Shape index	1.08	0.45	0.20	1.97	2.94	1.22	7.17	0.30
	SHDI	0.79	0.67	-0.53	2.11	2.20	0.59	8.25	0.18
	Mean forest patch size	0.25	0.11	0.04	0.45	1.28	1.04	1.57	0.13
	tt(mean forest patch size)	-0.09	0.04	-0.16	-0.01	0.91	0.85	0.99	0.13
	Contagion	-0.02	0.01	-0.04	0.00	0.98	0.96	1.00	0.09
	Grassland patch density	-0.04	0.02	-0.07	0.00	0.96	0.93	1.00	0.06
	Mean grassland patch size	0.03	0.03	-0.03	0.08	1.03	0.97	1.08	0.05
	Mean CRP patch area	0.01	0.02	-0.03	0.06	1.01	0.97	1.06	0.05
	Percent grassland	0.00	0.01	-0.01	0.02	1.00	0.99	1.02	0.03
	Mean crop patch area	0.00	0.03	-0.05	0.05	1.00	0.95	1.05	0.03

	Home range size	0.01	0.01	0.00	0.02	1.01	1.00	1.02	0.02
Ozarks	Percent grassland	-0.02	0.01	-0.04	-0.01	0.98	0.96	0.99	0.83
	Grassland patch density	0.21	0.08	0.06	0.36	1.23	1.08	1.43	0.76
	tt(Grassland patch density)	-0.08	0.03	-0.13	-0.02	0.92	0.88	0.98	0.76

[a] SHDI = Shannons' diversity index, CRP = Grasslands enrolled in the Conservation Reserve Program, tt() = log time interaction included in the model to account for the proportional hazards violation of these parameters.

[b] HR = Hazard ratio, calculated by taking the natural exponent of the β estimate. HR <1 indicated an increase in survival as the absolute value of the predictor value increased.

FIGURES

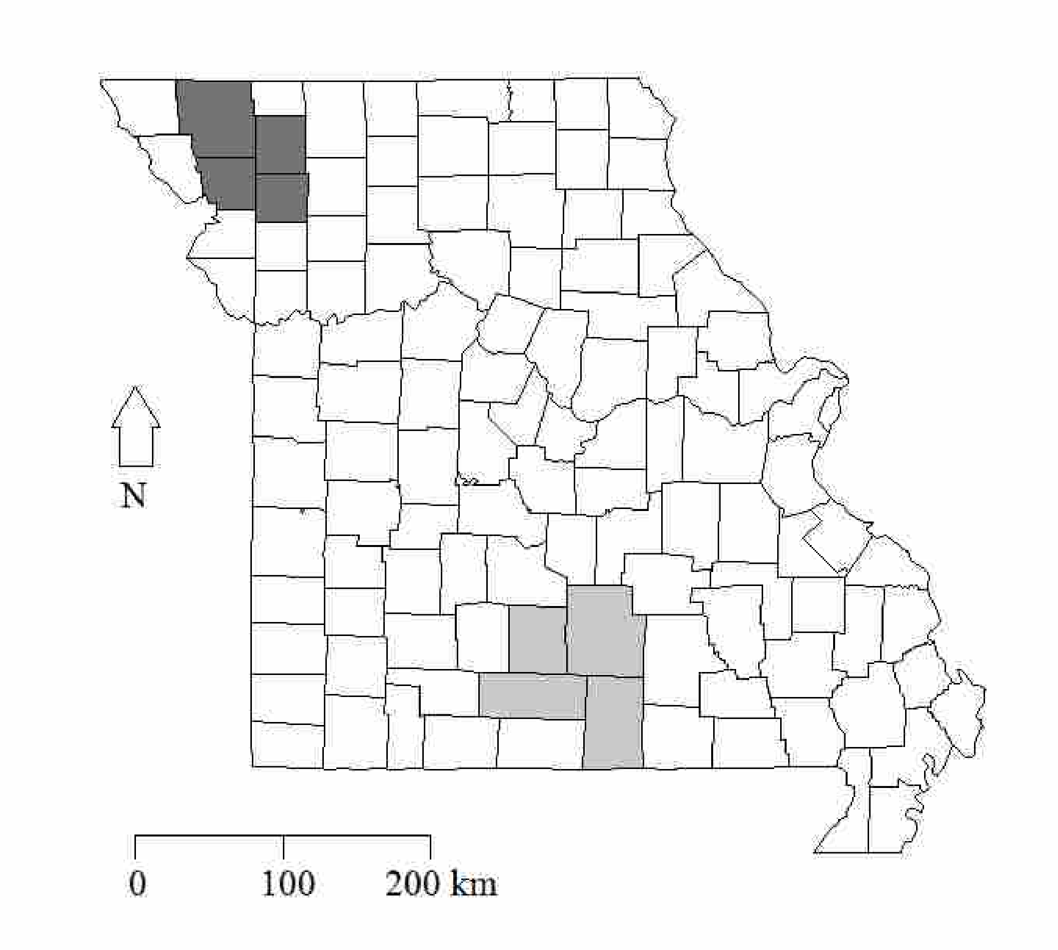

Figure 1. Map of the two study areas in Missouri, USA. The Glaciated Plains study area is shaded in dark grey and the Ozark study area is shaded in light grey.

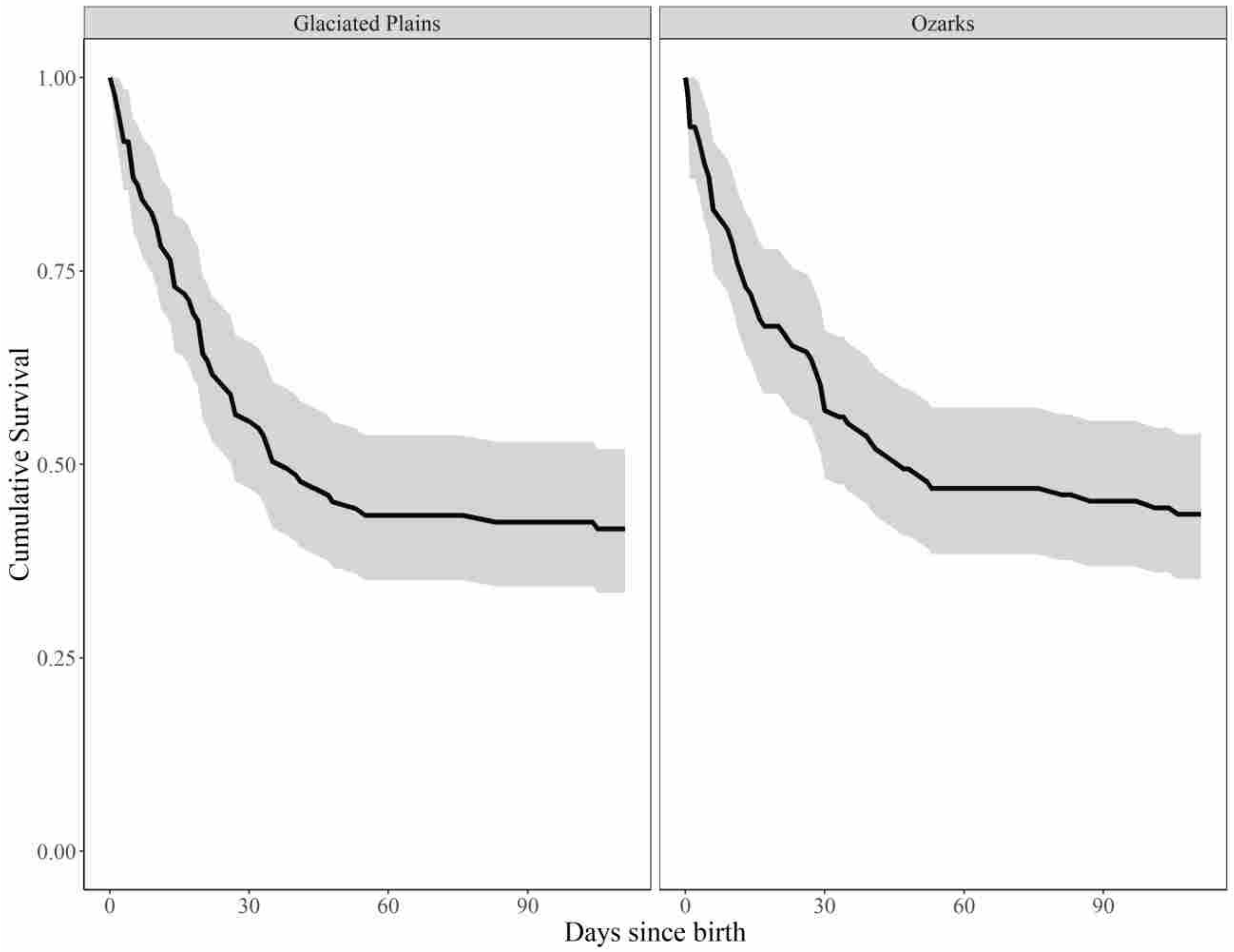

Figure 2. Survivorship curves based on the Kaplan-Meier estimator for radio-collared neonatal white-tailed deer from birth to 16 weeks of age in the Glaciated Plains and Ozark eco-regions of Missouri, USA, 2015 – 2017. Shaded areas indicate the 95% confidence interval.

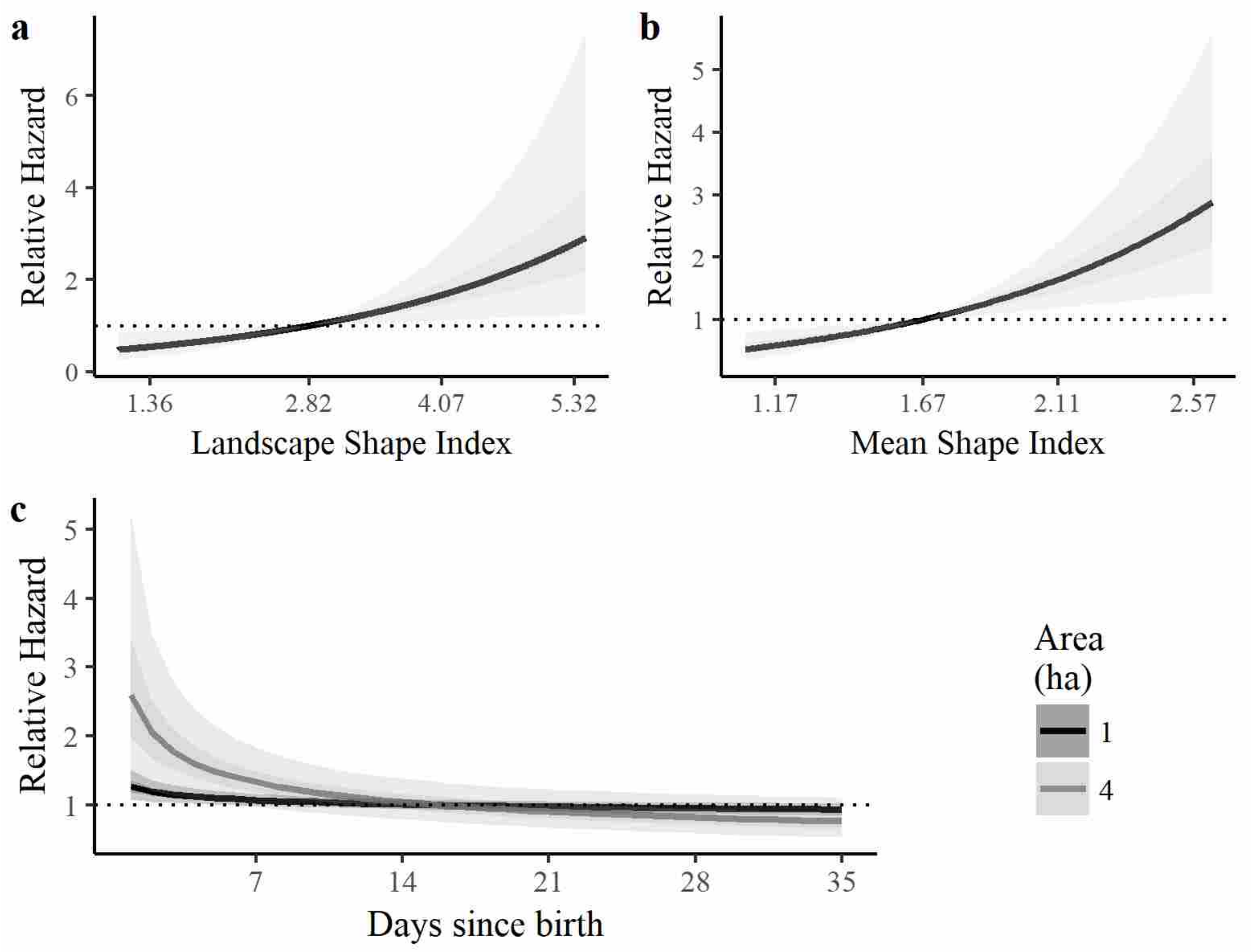

Figure 3. Simulation of the effects of informative landscape and class scale predictors of neonatal white-tailed deer survival in the Glaciated Plains region of Missouri, USA, 2015 – 2017. The extent of predictions was limited to extent of observed values for figures 3a and 3b. Light gray ribbons represent the 90% confidence interval, and dark gray ribbons represent the 50% confidence interval. Dotted lines at y=1 shows where hazards are equal. A) Relative hazard of mortality for a neonate within a home range with a landscape shape index value of 2.82 (the median value observed) compared to other values. B) Relative hazard of mortality for neonates within a home range with a mean shape index value of 1.67 (the median value) compared to other values. C) Relative hazard of mortality neonates within a home range with an average

forest patch size of 1 ha compared to 4 ha over time; this figure shows the non-proportionality of forest patch size, and the diminishing effect of forest patch size on mortality as neonates age.

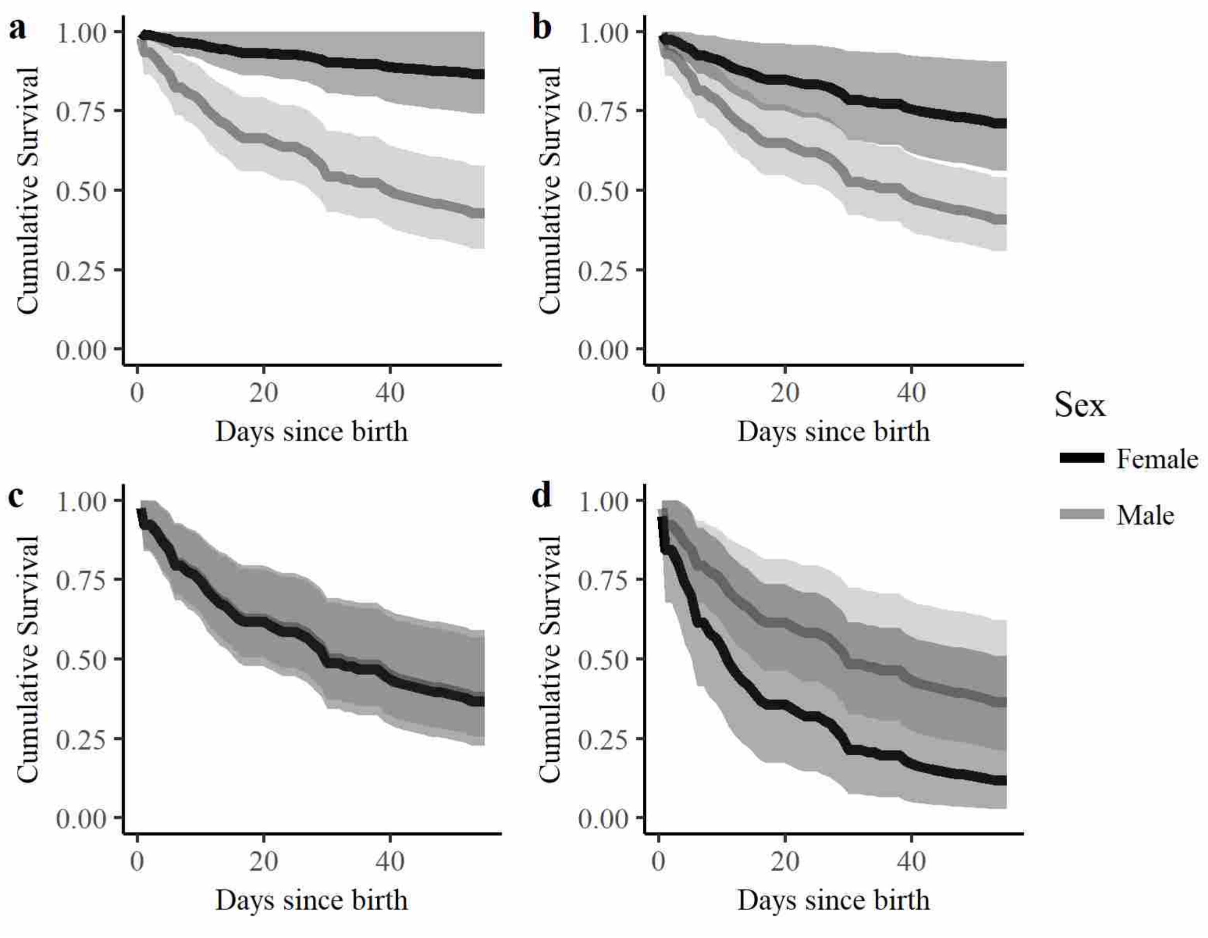

Figure 4. Predicted survival curves based on the most parsimonious Cox proportional hazards model (sex × mass) for explaining neonatal white-tailed deer survival to 55 days in the Ozark region of Missouri, USA, 2015 – 2017. Shaded areas show 95% confidence intervals. a) Survival estimates for male and female neonates born with a birth mass of 3.2 kg b) Survival estimates for male and female neonates born with a birth mass of 2.8 kg c) Survival estimates for male and female neonates born with a birth mass of 2.3 kg d) Survival estimates for male and female neonates born with a birth mass of 1.8 kg.

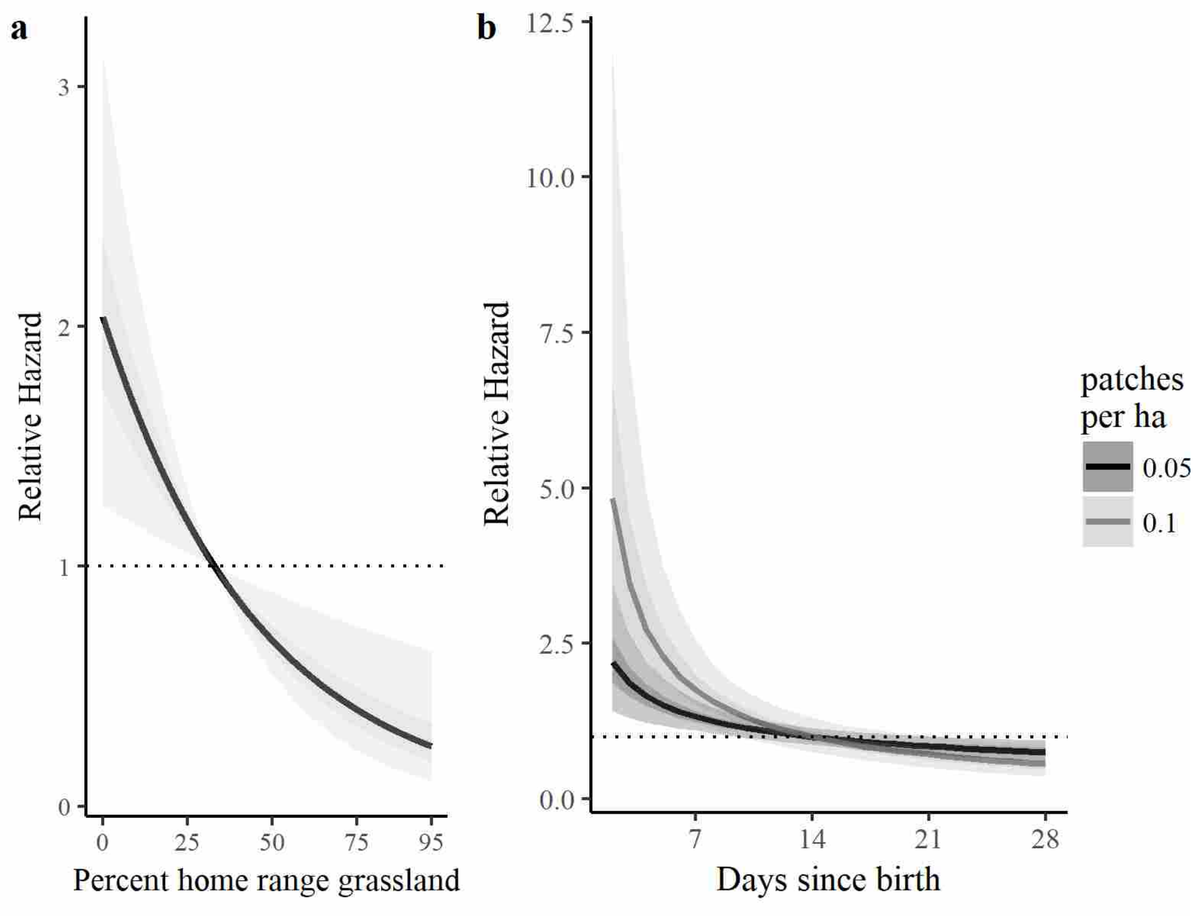

Figure 5. Simulation of the effects of informative landscape and class scale predictors of neonatal white-tailed deer survival in the Ozark region of Missouri, USA, 2015 – 2017. Light gray ribbons represent the 90% confidence interval, and dark gray ribbons represent the 50% confidence interval. Dotted lines at y=1 shows where hazards are equal. A) Relative hazard of mortality for neonates within a home range that is 33.61% grassland (the median value), compared to other values. B) Relative hazard of mortality for neonates within a home range that has 0.05 grassland patches per hectare compared to 0.1 grassland patches per hectare over time; this figure shows the non-proportionality of grassland patch density, and the diminishing effect of grassland patch density on mortality as neonates age.

Chapter 2: Female white-tailed deer (*Odocoileus virginianus*) behavior during pregnancy, parturition, and lactation in two different eco-regions of Missouri.

ABSTRACT

Late gestation, parturition, and lactation are the most metabolically expensive time periods in a female ungulate's life cycle, and also a time when females sometimes make trade-offs between acquiring sufficient forage and increasing the survival probability of their neonates. Females can also alter their movement patterns drastically depending on the stage of parturition. We evaluated how differences in land use, habitat types, predator species, and habitat fragmentation affected white-tailed deer (*Odocoileus virginianus*) space use, movements, and resource selection before, during, and after parturition in the highly fragmented glaciated plains (GP) and more contiguous Ozark (OZ) eco-regions of Missouri. We captured 135 pregnant female deer from January – March 2015-17, fitted them with global positioning satellite (GPS) radio-collars, and determined if their fawns survived using neonate radio-collars. We created weekly dam home ranges using the dynamic Brownian bridge movement model, calculated space use shifts, measured movement speed, and estimated resource selection for dams that had a live neonate during that week. Before parturition pregnant dams in both study areas maintained stable movement speeds until the week of parturition when crepuscular movement speeds decreased by 49.58% in the GP and 31.11% in the OZ. Home range sizes were over 150% smaller during the week of parturition compared to the third week before parturition in both study areas. Females shifted their space use 144.78 m (95% confidence interval [CI] 83.02 m – 252.22 m) in the GP and 162.89 m (95% CI 103.28 m – 256.74 m) in the OZ between the week before parturition and the week of parturition. Females in both study areas did not shift their resource selection before, during, and after parturition with the exception of site aspect. Females consistently selected for conservation reserve program (CRP) grasslands in the GP and deciduous forests in the OZ. We hypothesize that these habitats could provide suitable forage for the dam and adequate cover for the neonate, and thus were selected for both pre and post parturition. The similarity in behavior shifts, lack of resource selection changes, and a lack of movement to locate birth sites in the 2 study areas suggests that white-tailed deer may not have specialized habitat requirements for pregnancy and lactation in Midwestern habitats similar to our study areas. Enrollment in CRP is declining in the United States, but given the consistent selection for CRP that we observed in the GP, we recommend that managers place an emphasis on maintaining current levels of CRP, or planting habitat with similar functional attributes.

KEY WORDS white-tailed deer, parturition, resource selection, movement behavior, Missouri, *Odocoileus virginianus*, home range, dynamic Brownian bridge movement model, Bayesian discrete choice.

INTRODUCTION

Ungulate life history strategies are shaped by many factors, including the need to acquire energy while avoiding predation (Kie 1999). Late gestation, parturition, and lactation are the most metabolically expensive time periods in a female ungulate’s life cycle, with females needing to acquire maximal energy during this time period or face declines in body condition (Hewitt 2011). Furthermore, females must balance energy acquisition for their current offspring to survive against their own probability of surviving and reproducing again in the future (Trivers 1974, Stearns 1992, Regan et al. 2017). Consequently, females occupying diverse landscapes often make complicated tradeoffs between forage acquisition and avoiding predation, which could vary depending on the stage of reproduction (Rachlow and Bowyer 1998, Bongi et al. 2008, Long et al. 2009).

The energetic cost of gestation is minimal during winter (Hewitt 2011), but during the final trimester of gestation energetic investment in the developing fetus is maximized (Barboza and Bowyer 2000, Hewitt 2011). Furthermore, female susceptibility to predation is at its lowest during late gestation because they do not have young at heel (Berger 1991). Therefore, during the last few weeks of gestation pregnant females should select for habitats that have high nutritional quality to increase their body and fetus condition during this late stage of pregnancy (Barboza and Bowyer 2000, Long et al. 2009). Immediately following parturition the nutritional requirements for lactating females increase and peak roughly 10 – 37 days following birth (Sadleir 1980); peak lactation may cost females up to 470 kcal/kg$^{0.75}$/day, or 6.7 times their basal metabolic rate (National Research Council 2007, Hewitt 2011). Immediately following parturition is also the time period in which neonates are most susceptible to predation (Rohm et al. 2007, Shuman et al. 2017). This simultaneous increase in nutritional demands for the dam and predation threat for the neonates can restrict the ability of dams to successfully rear young (Bowyer et al. 1999). Understanding how females alter their behavior to cope with these often conflicting requirements can provide important insight into the evolution of ungulate life history strategies.

In some systems females select habitats that reduce predation risk to their young even though it comes at the expense of better foraging opportunities for themselves (Berger 1991, Ciuti et al. 2006, 2009, Hamel and Cote 2007). For example, Ciuti et al. (2006) found that maternal fallow deer (*Dama dama*) selected for marsh habitat following parturition while non-maternal females selected for meadow habitat, which contained the most nutritious resources for deer in their study area. However, grass height in the meadow habitat rarely exceeded 20 cm thus making it inadequate hiding cover for neonates, unlike the tall, dense vegetation that characterized the marsh habitat (Ciuti et al. 2006). In other systems where females are more energetically stressed they may use more risky, but nutritionally superior areas and adopt scale-dependent antipredator responses to protect their neonates (Gustine et al. 2006, Ratikainen et al. 2007, Panzacchi et al. 2010). In south-eastern Norway Panzacchi et al. (2010) found that maternal roe deer (*Capreolus capreolus*) selected for meadows, which granted the highest nutritional gain despite the higher predation risk to neonates in these areas; the benefits related to access of high quality resources outweighed the cost of increases in predation risk. To combat this increased predation risk, mothers tried to maximize neonate survival by adjusting their behavior at the bed site to minimize their visibility to predators (Panzacchi et al. 2010).

In addition to altering resource selection depending on the stage of reproduction, females make changes in their movement patterns (Ozoga et al. 1982, Vore and Schmidt 2001, DeMars et al. 2013). In the weeks leading up to parturition movement rates and space use are similar between pregnant and non-pregnant females (Vore and Schmidt 2001, Ciuti et al. 2006, Bongi et al. 2008). Pregnant individuals of some species, such as elk (*Cervus canadensis*) and moose (*Alces alces*), dramatically increase their daily movement distances 2 – 4 days before parturition (Vore and Schmidt 2001, Poole et al. 2007, Severud et al. 2015). This increase in movement is usually directional in nature and is thought to be the mother searching for a parturition site with adequate cover in which to give birth and protect the neonate from predation (Testa et al. 2000).

The presence of a neonate changes the social organization and spatial behavior of females (Ozoga et al. 1982, Schwede et al. 1993, Bertrand et al. 1996). Mothers tend to isolate themselves from conspecifics around the time of parturition, which is considered to be essential for the formation of mother-infant bonds, and serves as an additional protective measure against predation (Lent 1974, Ozoga et al. 1982). The degree and duration of isolation depends largely on the species, but it appears to be a general rule among ungulates (Altmann 1963, Ozoga et al. 1982, Vore and Schmidt 2001, Karsch et al. 2016). As a result of this isolation and the limited mobility of neonates, maternal females may reduce the size of their home ranges and decrease movement rates (D’Angelo et al. 2004, Ciuti et al. 2006, Bongi et al. 2008, Long et al. 2009). Some studies have used fine scale movement data to accurately determine the date of parturition because reductions in movements are so extreme at this time (DeMars et al. 2013, Severud et al. 2015).

There are many factors that influence how female ungulates alter their behavior in response to parturition including differences between life history traits of specific species, abundance and type of predators present, and differences in habitat (Ciuti et al. 2006, Gustine et al. 2006, Panzacchi et al. 2010, Karsch et al. 2016). Many studies have investigated changes in female behavior surrounding parturition but most were conducted in only one study region, thus making direct comparisons about how these factors influence behavior difficult (Vore and Schmidt 2001, Ciuti et al. 2006, Bongi et al. 2008, Long et al. 2009). Our objective was to determine how female white-tailed deer (*Odocoileus virginianus*) altered their resource selection, space use, and movement rates before and after parturition in the Glaciated Plains (GP) and Ozark (OZ) eco-regions of Missouri. These regions differed in land ownership, land use, predator species, and habitat composition and fragmentation, allowing us to determine how these factors might impact pregnant and lactating female deer behavior. We predicted that in both areas pregnant females would significantly reduce their space use and movement rates during parturition, but females in the more fragmented region (GP) would exhibit greater space use and movement rates overall than those in the area with more contiguous forested cover (OZ). We also predicted that females in the OZ would select for grasslands pre-parturition because of their greater nutritional quality and select for steeper slopes and forested cover post-parturition. In the GP we predicted that females would select for crop habitats pre-parturition, because of their greater nutritional quality, and select for forested cover and conservation reserve program (CRP) grasses post-parturition as cover for their neonates.

STUDY AREAS

Glaciated Plains

The Glaciated Plains (GP) eco-region encompasses 32% of Missouri and is characterized by rich, productive soils. The GP study area included Andrew, Gentry, DeKalb, and Nodaway counties in northwest Missouri (Figure 1). The combined area of the 4 counties was 5779.29 km^2 and is 2.48% urban areas, 44.50% cultivated crops, 12.26% forest, 37.73% grassland, and 3.03% other. Land enrolled in the Conservation Reserve Program (CRP) made up 19.07% of the grassland vegetation (USDA Farm Service Agency [FSA] 2017). Publicly owned land made up 1.28% of the total area and was mostly comprised of conservation areas owned by the Missouri Department of Conservation (MDC). The most common land uses were farming of cultivated crops, with corn and soybeans totaling 36.98% and 50.86% of all crops grown, respectively, and raising cattle for beef and dairy production. The area was also characterized by low, rolling hills with elevation ranging from 185 m to 475 m, with local relief from 3 m to 30 m (United States Department of Agriculture [USDA] Natural Resources Conservation Service [NRCS] 2006).

The climate consisted of moderately cold winters and warm, humid summers. The mean annual temperature was 11.3^{o} C, with minimum temperatures in January (-8.86^{o} C) and highest temperatures in July (30.52^{o} C; Prism Climate Group). The average annual precipitation was

94.36 cm, with the lowest precipitation in January (2.1 cm) and the highest in June (13.04 cm; Prism Climate Group).

Land not dominated by agriculture supported grassland vegetation and oak-hickory forest (NRCS USDA 2006). Common grass species included big bluestem (*Andropogon gerardi),* indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium),* switchgrass *(Panicum virgatum),* and wildrye *(Elymus* spp.*).* Upland wooded areas supported southern red oak *(Quercus falcata*), white oak *(Q. alba*), hackberry *(Celtis* spp.*),* shagbark hickory *(Carya ovata*), and bitternut hickory *(C. cordiformis).* Bottomland wooded areas included sycamore *(Platanus occidentalis),* cottonwood *(Populus* spp.), elms *(Ulmus* spp.), green ash *(Fraxinus pennsylvanica*), and silver maple *(Acer saccharinum).* At the time of this study deer density in the 4 county area was approximately 7 deer/km^2 (K. Wiskirchen, Missouri Department of Conservation, personal communication). Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) were the two most common predators, with 5 confirmed mountain lion (*Puma concolor*) sightings in the GP since 2006.

Ozarks

The Ozark (OZ) eco-region encompassed 38% of Missouri and was characterized by thin, rocky soils. The OZ study area included Douglas, Howell, Texas, and Wright counties in south-central Missouri (Figure 1). The combined area of the 4 counties was 9,332.25 km^2 and was 2.09% urban areas, 1.69% cultivated crops, 52.65% forest, 42.98% grassland, and 0.59% other. Publicly owned land comprised 14% of the Ozark region and the 4 county area included 600 km^2 of Mark Twain National Forest. The most common land use was the raising of cattle for beef and dairy production, with a total of 3,766 farms with 279,868 head of cattle throughout the four counties (USDA National Agricultural Statistics Service [NASS] 2012). The topography was highly variable, with elevation ranging from 90 m to 500 m and local relief anywhere from 60 m to 240 m (Thom and Wilson 1980, NRCS USDA 2006). Caves, springs, bluffs, and clear-flowing streams were characteristic features of the area.

The climate consisted of moderately cold winters and warm, humid summers. The mean annual temperature was 13.26^{o} C, with minimum temperatures in January (-5.39^{o} C) and high temperatures in August (31.5^{o} C; Prism Climate Group). The average annual precipitation was 115.11 cm, with the lowest precipitation in January (6.63 cm) and the highest in May (12.72 cm; Prism Climate Group).

The OZ was mostly oak-hickory and oak-hickory-pine forests (NRCS USDA 2006). The dominant tree species were black oak (*Quercus velutina*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), post oak (*Q. stellata*), hickory (*Carya* spp.), and shortleaf pine (*Pinus echinata*). Most non-forested areas were created for pasture or hay fields, but some natural glades occurred and supported warm-season grasses, such as big bluestem, indiangrass, and little bluestem. At the time of this study, deer density in the 4 county area was approximately 9 deer/km^2 (K. Wiskirchen, personal communication). Coyotes and bobcats were the predominant predators in the area, although a small, recolonizing black bear (*Ursus americanus*) population existed in the southern OZ region. There have been < 45 confirmed mountain lion sightings in the entire OZ region since 2006.

METHODS

Adult White-tailed Deer Capture

We captured fawn (6-9 month old), yearling (1.5 year old), and adult (>1.5 years old) female deer using modified Clover traps (VerCauteren et al. 1999) and rocket nets (Haulton et al. 2001) from January – March 2015 – 2017. Adult and yearling females were immobilized using Telazol (Tiletamine hydrochloride HCl and zolazepam HCl, 4.4 mg/kg) and xylazine HCl (2.2

mg/kg; Kreeger et al. 1996, Kilpatrick and Spohr 1999) or BAM (Butorphanol Tartrate, Azaperone Tartrate, Medetomidine HCl; Wolfe et al. 2014). We determined pregnancy using a portable trans-abdominal ultrasound (Ibex Lite, E.I. Medical Imaging, Loveland, CO) and inserted a vaginal implant transmitter (VIT; Model M3930 Advanced Telemetry Systems, Inc., Isanti, MN) if the doe was pregnant (Bowman and Jacobson 1998). Captured deer received a uniquely numbered metal ear tag (Hasco Tag Company, Dayton, KY) and were fitted with a 825g Iridium GPS radio-collar (Model G2110E, Advanced Telemetry Systems) that was programmed to record a location every hour and upload locations daily at 0600 and 1800. Collars were equipped with an 8-hour motion sensitive switch that alerted us remotely when the collar remained motionless. We reversed the xylazine HCl with an intravenous injection of tolazoline (4.0 mg/kg; Miller et al. 2004) or reversed the BAM with an intramuscular injection of Atipamezole and Naltrexone HCl (Wolfe et al. 2014).

Due to logistical constraints not all yearling and adult females were chemically immobilized and checked for pregnancy in the field. Therefore we collected 1 mL to 5 mL of blood to check for pregnancy using pregnancy specific protein B (PSPB) levels (Duquette et al. 2012). All capture and handling procedures were approved by the Institutional Animal Care and Use Committee at the University of Missouri (protocol number 8216).

Determining date of parturition and pregnancy status

Collars were active for > 1 year post capture, so we used 2 metrics to determine if females were pregnant in years when we did not have current PSPB blood tests or ultrasound results: 1) if we caught and collared their neonate(s) that year (See Chapter 1 for details), 2) recruitment checks. We conducted recruitment checks September – October and used VHF telemetry to visually observe every collared female at least 3 times. If we saw the female with a fawn during at least 2 out of the 3 checks, we concluded they had a fawn that summer and thus were pregnant that year.

The parturition date for females that received a VIT was the date the VIT was expelled, if we located the VIT at a birth site (Bishop et al. 2011, Hasapes and Comer 2017). Females that we found a neonate for, but did not receive a VIT or expelled the VIT prematurely, were given an estimated date of parturition calculated by subtracting the estimated age of the neonate from the capture date (See Chapter 1). Females that we knew were pregnant due to their PSPB levels or recruitment checks, but we did not find a neonate for, were assigned the average parturition date for that respective year and study area.

Parturition periods

Pre-parturition was defined as the 3 weeks prior to the day the doe gave birth, parturition was the week the doe gave birth, and post-parturition was the 3 weeks after the week of parturition. Using 3 weeks of data on either side of parturition enabled us to investigate relationships between changes in behavior and the varying energetic demands related to late gestation and peak lactation (Long et al. 2009, Hewitt 2011). The week of parturition began on the estimated date of parturition and was referred to week as 0. The weeks before parturition were referred to as negative (e.g., -3 for the 3rd week before parturition) and weeks after parturition were referred to as positive.

Females alter their movements and select for resources differently when their fawns die (Ozoga et al. 1982, Testa et al. 2000, DeMars et al. 2013, Singh and Ericsson 2014). Therefore we only included females in the post-parturition analysis for a given week provided they had at least 1 neonate alive at the end of the week. The presence of a live neonate was determined by the mortality status of radio-collared fawns associated with radio-collared females (See chapter

1) and recruitment checks in the fall. Females were only included in the pre-parturition analysis for a given year if we knew they were pregnant that year.

Movement characteristics

We evaluated the influence of age, forest cover, time of day (crepuscular, day, night), and week relative to parturition on female deer movement speed. We excluded all collar locations where the GPS positional dilution of precision (PDOP) reading was > 10 (D'Eon and Delparte 2005) and locations that were taken > 24 hours apart. We calculated the time and distance between successive locations using the geosphere package (Hijmans et al. 2017*a*) in Program R version 3.4.3 (R Core Team 2017), and computed the movement speed in meters per hour. We used the maptools package (Bivand et al. 2017*a*) in program R to determine sunrise, sunset, start of nautical dawn, and nautical dusk at each specific location. We obtained the 2011 land use land cover (LULC) layer from the National Land Cover Database (NLCD; Homer et al. 2015) for all 8 study area counties and used the raster package (Hijmans et al. 2017*b*) in Program R to re-classify each pixel as forested (included deciduous, evergreen, mixed forests), or non-forested. We assigned each location as either forested or non-forested, and the time of day the location was taken: day, night, or crepuscular. Day time locations occurred from 1 hour after sunrise to 1 hour before sunset, night occurred from nautical dusk to nautical dawn, and crepuscular was nautical dawn to 1 hour after sunrise and 1 hour before sunset to nautical dusk. We did not capture enough pregnant yearling and fawn females to include as separate age classes in the analysis, so we classified deer as either adults (≥2 years old at the start of the analysis) or sub-adults (<2 years old at the start of the analysis).

We predicted that time of day would have the greatest influence on deer movement speed (Beier and McCullough 1990), with deer moving faster during crepuscular and night time hours than during the day (Webb et al. 2010). We also predicted that forested habitat would serve as cover and result in reduced deer movements (VerCauteren and Hygnstrom 1998). Finally, we predicted that deer movement speeds would be constant prior to parturition, decrease during the week of parturition, and slowly increase again post parturition (Long et al. 2009). To test these predictions we used the information theoretic approach (Burnham and Anderson 2002) to develop a set of candidate models for each study area (Table 1). We log transformed movement speed and ran each model as a linear mixed model with deer identification and year as random effects using the lme4 package (Bates et al. 2017) in Program R. We used Akaike's information criterion adjusted for small sample sizes (AIC_c) to determine the best model in the candidate set and considered models within 2 ΔAIC_c units as competing for the top model (Burnham and Anderson 2002). If models within this threshold only differed from the top model by one additional parameter we considered that parameter to be uninformative and unsupported by the data. We conducted model selection using the package AICcmodavg (Mazerolle 2017) in Program R.

Space use

To evaluate the influence of forest cover, landscape diversity, age, and week relative to parturition on female deer space use we calculated home ranges during each week using the dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012) using the move package (Kranstauber et al. 2017) in Program R. The dBBMM computes home ranges by creating a utilization distribution (UD; Worton 1989) that incorporates both the size of the area of use and the animal's intensity of use within this area. The dBBMM creates a UD by modeling the space use between 2 continuous locations as Brownian movement, a continuous random walk in which movement is diffusive and equally likely in any direction (Turchin 1998, Horne et al.

2007). The dBBMM requires the fixed position, time of each location, error associated with the locations (GPS collar error), and the degree to which movement between locations deviates from a straight line, also known as the magnitude of variance of the Brownian motion (σ_m^2). To account for behaviorally distinct movements that change over time, the dBBMM allows σ_m^2 to vary along the movement path (Gurarie et al. 2009, Kranstauber et al. 2012) using an adjusted version of the behavioral change point analysis (Gurarie et al. 2009) via a sliding window with *w* locations along a path. The window moves along the movement path and calculates a new σ_m^2 for each step every time it falls within the window. These σ_m^2 estimates are averaged to get a final σ_m^2estimate for each step.

Choosing the size of the window is a critical step because a tradeoff exists between the greater reliability in the estimation of σ_m^2 with a large window size and the short term changes that can be detected with a small window. Also, a margin (*m*) greater than 3 locations is needed on either end of the window in which no break points can occur. We used a window size of 7 (equivalent to 7 hours) and a margin of 3 that we chose based on the cross-validation techniques suggested by Kranstauber et al. (2012). We used a GPS collar error of 5.92 m that we determined by performing GPS collar accuracy field tests (Appendix A).

We used 95% volume contours to define the home range area (ha), and only estimated the home range area for deer during a week provided they had at least 4 days' worth of locations in that week. We used the same forest layers developed for the movement speed analysis, and used the SDMTools package (VanDerWal et al. 2014) in Program R to compute the proportion of each home range that was forested (0 – no forest, 1 – completely forested). We reclassified the 2011 NLCD land cover layer to the most common habitat types within our study areas (Table 2). We clipped the re-classified land use layer to each weekly doe home range and used

FRAGSTATS version 4.2 (McGarigal et al. 2012) to calculate the diversity of land cover types within each home range, as measured by the Shannon's diversity index (SHDI; McGarigal et al. 2012). We aged deer in the same manner as before, and assigned each home range to its respective week of parturition.

We predicted that forest land cover would act as cover habitat, and thus reduce home range sizes in both study areas (Harlow 1984, Long et al. 2005). We also predicted that as diversity of the home range increased, home range sizes would decrease because of increased availability of resources, and increased amounts of edge (Kie et al. 2002). Finally, we predicted that home range sizes would be constant prior to parturition, decrease sharply during parturition, and slowly increase in size post-parturition (Ciuti et al. 2006). To test these predictions we used the information theoretic approach (Burnham and Anderson 2002) to develop a set of 19 candidate models in each study area (Table 3). We log transformed home range size and ran each model as a linear mixed model with deer identification and year as random effects using the lme4 package (Bates et al. 2017) in Program R. We selected the best approximating model using AIC_c (Burnham and Anderson 2002) using the AICcmodavg package (Mazerolle 2017) in Program R as described in the movement speed section.

We calculated the distance between home range centroids to evaluate shifts in space use before, during and after parturition (Kernohan et al. 2001). We suspected that home range sizes would reduce significantly during the 7 week period, so we did not want to calculate space use overlap metrics that would be confounded by a reduction in space use. We calculated the distance between the centers of successive weekly home ranges using the rgeos (Bivand et al. 2017*b*) package in program R. We created 5 models that we thought would best explain the variation in distances between home range centers and included age of the deer, the comparison made, and the additive and interactive forms of these as covariates. We log transformed the distances and then ran each model as a linear mixed model with deer identification and year as random effects using the lme4 package (Bates et al. 2017) in Program R. We selected the best approximating model using AIC$_c$ (Burnham and Anderson 2002) in the AICcmodavg package (Mazerolle 2017), as described above.

Resource selection

We determined third order resource selection (within home range; Johnson 1980) for female deer before, during, and after parturition (not on a weekly basis) by comparing resource attributes at points where deer were located (used locations) to attributes at random points that were considered available (available locations). Defining resource availability is a critical component of a resource selection analysis (Buskirk and Millspaugh 2006). We uniquely defined availability at each used point to ensure that all the resources classified as available were available to the animal at that time; this is known as creating a choice set (Cooper and Millspaugh 1999). We determined availability by selecting 5 random points within a circle created using the radius of available habitat method (Durner et al. 2009). This method creates a circle centered on the deer's previous location using the equation

$$radius\ of\ avilable\ habitat = c(a + 2b)$$

where a is the mean hourly movement rate, b is the standard deviation of the movement rate and c is the number of hours between locations (Durner et al. 2009). We calculated the mean hourly movement rate for the 3 different parturition periods in each study area to account for differential movement rates during these times (Long et al. 2009). If the used location occurred outside of the circle created using this method, we defined the radius as the straight line distance between the previous and used location (Durner et al. 2009). We used the geosphere package (Hijmans et al. 2017*a*) in Program R to calculate the movement rates and hours between locations.

We defined 9 resource attributes within 30-m X 30-m cells which we called resource units (Table 4). We used the LULC layer downloaded previously and reclassified it into the 6 most commonly used land cover types in each study area (Table 2). We calculated contagion, which measures the degree to which patch types of the same land cover type are clumped together, using FRAGSTATS version 4.2 (McGarigal et al. 2012). We calculated contagion within a circle defined by the average radius of available habitat for all deer (Durner et al. 2009). To determine if deer selected for areas closer to cover we calculated the distance to the nearest wooded edge. We used the geospatial modeling environment (GME; Beyer 2012) to extract the edges between forests and open areas from the LULC layer and then used the rgeos package (Bivand et al. 2017*b*) in Program R to determine the distance to edge.

We obtained the 2011 percent canopy cover layer from the USFS NLCD and 10 m demographic elevation models (DEM) for all 8 study area counties from the USDA Geospatial Data Gateway. We used Surface Tools in ArcGIS 10.3 (Environment Research System Institute Inc., Redlands, CA) to calculate aspect class (north, east) and slope (degrees) from the DEM's. We calculated road density and distance to road to account for potential human disturbance. We calculated road density as meters of roads per square meter contained within a circle with a radius equal to the mean radius of available habitat to deer in each study area using the rgeos package (Bivand et al. 2017*b*) in Program R. We acquired our road layers using TIGER 2016 road data acquired from the US Census Bureau.

We modeled resource selection with hierarchical Bayesian discrete choice models (Cooper and Millspaugh 1999, Thomas et al. 2006). The observational units in this study were the choice set (i.e., the used location and the available alternative choices associated with each used location). We assumed the location selected from choice set *i* by deer *j* was a multinomial random variable:

$$y_{ij} \sim Multinomial(\pi_{ij}, 1)$$

where y_{ij} is a K_{ij}-dimensional vector of 0s (available locations) and 1 (used location), K_{ij} is the number of used and available alternatives in choice set *i*, and π_{ij} is a K_{ij}-dimensional vector denoting the probability of selecting any of the alternatives in choice set $i\left(\sum_{k=1}^{K_i}\pi_{ijk} = 1\right)$. We assumed a latent utility associated with each used and available alternative:

$$u_{ij} = x'_{ijk}\beta_j$$

where x_{ijk} is an *L*-dimensional vector of variables associated with alternative *k*, and β_j is a conformable vector of slope parameters unique to deer *j*. We assume random slope coefficients for each deer by modeling each element $l = 1, \ldots, L$ of β_j hierarchically:

$$\beta_{jl} \sim Normal(\mu_{jl}, \sigma_l^2)$$

where μ_{jl} and σ_l^2 are the population-level mean and variance, respectively, of slope coefficients associated with variable *l*. We allowed the mean of individual-level slope coefficients to vary as a function of week of parturition by modeling the population-level mean of slope coefficient *l* as:

$$\mu_l = S\theta_l$$

where S is a $J \times M$ design matrix, *J* indicates the number of unique combinations of individual deer by period of parturition, *M* indicates the number of parameters in the population-level mean model ($M = 3$: intercept; 2 period of parturition parameters), and θ_l is a conformable vector of parameters. We calculated the probability deer *j* selected alternative *k* within choice set *i* as a function of the latent utility:

$$\pi_{ijk} = \frac{\exp(u_{ijk})}{\sum_{a=1}^{K_i} \exp(\mu_{ija})}$$

We assumed the following prior distributions:

$$\theta_l \sim Multivariate\ Normal(0, I)$$

$$\sigma_l^2 \sim Inverse\ Gamma\ (1,1)$$

We evaluated goodness of fit of the model with posterior predictive checks (Kéry and Schaub 2012, Gelman et al. 2014). We calculated the deviance function (McCullagh and Nelder 1989) from observed data (T_y) and from data simulated assuming the model was the data-generating model (T_{rep}). We then calculated a Bayesian p-value $p_B = \Pr(T_{rep} > T_y)$ from posterior simulations and assumed reasonable fit if $0.1 < p_B < 0.9$. We did not conduct model selection to determine a top model but rather based inference on habitat selection from the posterior distribution of the population-level μ_l and its 95% credible interval using a global model. Specifically, we interpreted predictors with 95% credible intervals that did not overlap 0 as important variables in the habitat selection model (Beatty et al. 2014).

We conducted posterior sampling with Stan v. 2.17.0 (Stan Development Team 2017a), implemented in R via the RStan v. 2.16.2 interface (Stan Development Team 2017b). We simulated 3 posterior chains for each model, running each chain until adequate convergence was achieved ($\hat{R} \leq 1.1$, Gelman et al. 2014). We thus ran each chain for 10,000 iterations, discarding the 1st 1,000 iterations as warm-up and keeping the remaining 9,000 iterations.

RESULTS

During 2015 – 2017 we caught and tested for pregnancy in 348 female fawn, yearling, and adult deer (Table 5). Overall fawn pregnancy rates were 16.67% (n = 8/48) in the GP, and 8.86% (n = 7/79) in the OZ. Yearling pregnancy rates were 100% (n= 14/14) in the GP, and 95.00% (n =

38/40) in the OZ, and adult pregnancy rates were 98.41% (n = 62/63) in the GP, and 98.08% (n = 102/104) in the OZ. We marked 135 pregnant female fawn, yearling, and adult deer (2015: 22 GP, 25 OZ; 2016: 22 GP, 29 OZ; 2017: 19 GP, 18 OZ) with GPS collars. We included 38 of these females in 2 years of the analysis and 3 females in all 3 years of the analysis (Table 6). Average dates of parturition were 27 May 2015, 29 May 2016, and 27 May 2017 in the GP, and 23 May 2015, 29 May 2016, and 23 May 2017 in the OZ.

Movement and space use metrics

Glaciated Plains – Differences in movement speeds were best explained by the time of day the movement occurred, whether the movement began in a forested or non-forested location, and the week relative to parturition in which the movement occurred (Table 7, Figure 2). Crepuscular movement speeds were faster than both day and night speeds, and speeds were constant prior to parturition. During the week of parturition dams decreased their crepuscular speeds by 49.58% and increased their day and night movement speeds by 18.97% and 13.86%, respectively (Table 7, Figure 2). Movement speeds slowly increased after parturition. Differences in home range sizes were most explained by the week relative to parturition and the SHDI; home ranges with a bigger SHDI value were larger in size (Figure 3). Before parturition home range sizes slowly declined and by the week of parturition home range sizes were 178.66% smaller compared to the third week before parturition (Figure 4). The distance between home range centroids was the largest between the week before parturition and the week of parturition, but this distance was only 144.78 m (95% confidence interval [CI] 83.02 m – 252.22 m; Figure 5).

We considered time of day × week of parturition + forest ($\omega_i = 0.62$) as the top supported model for movement speed. The second most supported model was time of day × week of parturition + forest + age ($\omega_i = 0.38$, $\Delta AIC_c = 0.96$) but the additional age covariate was not informative (β = 0.03, 95% CI = -0.03 – 0.09), thus we considered this model uninformative. The rest of the models were ≥ 37.32 ΔAIC_c away from these 2 models. Females moved 7.24% slower in forested areas compared to non-forested areas and moved faster during crepuscular hours compared to day and night, but the magnitude of this difference depended on the week relative to parturition (Table 7, Figure 2). Dams in forested areas decreased their crepuscular speeds from 74.74 mph (95% CI = 63.16 mph – 88.44 mph [meters per hour]) in week -3 to 49.97 mph (95% CI = 42.11 mph – 59.27 mph) during week 0 (Table 7, Figure 2). After the week of parturition females increased their crepuscular movement speeds slightly each week, and by week 3 these speeds were only 27.30% lower than week -1 (Table 7, Figure 2).

We considered week of parturition + diversity ($\omega_i = 0.55$) to be the most supported model for home range size. The second most supported model was week of parturition + diversity + age ($\Delta AIC_c = 0.43$, $\omega_i = 0.43$), but the additional age covariate was not informative (β = 0.23, 95% CI = -0.05 – 0.50). The rest of the models were ≥ 8.32 ΔAIC_c from the top model. Observed Shannon's diversity index (SHDI) values ranged from 0 (home range was only 1 habitat type) to 1.55 (all habitat types present in roughly equal proportions). Increasing SHDI by 0.5 correlated with an increase of 69.02% in home range size (β = 1.05, 95% CI = 0.82 – 1.28; Figure 3). Home range sizes decreased from 44.48 ha (95% CI = 22.52 ha – 87.87 ha) during week 3 to 15.96 ha (95% CI = 8.02 ha – 31.74 ha) during week 0, as measured with the mean observed SHDI value (β = -1.02, 95% CI = -1.17 – -0.88; Figure 4). Home range sizes increased by 10.87% from week 0 to week 1 (β = -0.92, 95% CI = -1.07– -0.78), increased an additional 23.31% from week 1 to week 2 (β = -0.71, 95% CI = -0.86 – -0.57), and 20.41% from week 2 to week 3 (β = -0.27, 95% CI = -0.41 – -0.12). Home range sizes in week 3 were 69.28% smaller than in week -3 (Figure 4).

The distance between weekly home range centers was best explained by the week of parturition (ω_i = 0.57). The second most supported model was week of parturition + age (ω_i = 0.42, ΔAIC_c = 0.42), but the additional age parameter was not informative (β = 0.19, 95% CI = -0.11 – 0.49). The rest of the models were ≥ 7.95 ΔAIC_c from the top model. The distance between the home range centers of week 0 and week -1 was 76.40% greater than the distance between the home range centers of week -1 and -2 (β = 0.56, 95% CI = 0.27 – 0.86; Figure 5). The distances between the centers of the other weeks were not different (week -3 vs. week -2: β = 0.08, 95% CI = -0.21 – 0.36; week -2 vs. week -1: β = 0.01, 95% CI = -0.29 – 0.28; week 0 vs. week 1: β = 0.06, 95% CI = -0.24 – 0.37; week 1 vs. week 2: β = -0.01, 95% CI = -0.31 – 0.30).

Ozarks – Differences in movement speeds were most explained by the time of day the movement occurred, whether the movement began in a forested or non-forested location, and the week relative to parturition in which the movement occurred (Table 8, Figure 6). Crepuscular movement speeds were faster than both day and night speeds, and speeds were constant prior to parturition. Females reduced their crepuscular movement speeds by 31.11% and increased their day and night movement speeds by 14.19% and 13.78% respectively, between the week before parturition and the week of parturition (Table 8, Figure 6). Crepuscular movement speeds increased after parturition and by the third week after parturition were similar to pre-parturition speeds. Differences in home range sizes were most explained by the week relative to parturition and the SHDI; home ranges with a bigger SHDI value were larger in size (Figure 7). Before parturition home range sizes slowly declined and by the week of parturition home range sizes were 178.47% smaller compared to the third week before parturition (Figure 8). The distance between home range centroids was the largest between the week before parturition and the week of parturition, but this distance was only 162.89 m (95% CI 103.28 m – 256.74 m; Figure 5).

We considered time of day × week of parturition + forest ($\omega_i = 0.72$) as the top supported model for movement speed. The second most supported model was time of day × week of parturition + forest + age ($\omega_i = 0.28$, $\Delta AIC_c = 1.86$) but the additional age covariate was not informative ($\beta = -0.01$, 95% CI = -0.08 – 0.05). The rest of the models were ≥ 40.30 ΔAIC_c away from the top model. Females moved 6.70% faster in forested areas compared to non-forested areas and moved faster during crepuscular hours compared to day and night, but the magnitude of this difference depended on the week relative to parturition (Table 8, Figure 6). Females reduced their crepuscular movement speeds in non-forested areas from 63.09 mph (95% CI = 56.21 mph – 70.80 mph) in week -3 to 48.11mph (95% CI = 42.80 mph – 54.06 mph) in week 0 (Table 8, Figure 6). After the week of parturition females increased their crepuscular movement speeds each week, and by week 2 these speeds were similar speeds prior to parturition (Table 8, Figure 6).

The most supported model for home range size was week of parturition × diversity (ω_i = 0.36, number of parameters [K] = 17); the second most supported model was week of parturition + diversity ($\omega_i = 0.30$, $\Delta AIC_c = 0.41$, K = 11). Given that the top model had an additional 6 parameters but was less than 1 ΔAIC_c from the second model, we considered week of parturition + diversity as the top model. The second and third best models were week of parturition × diversity + age ($\omega_i = 0.17$, $\Delta AIC_c = 1.50$) and week of parturition + diversity + age ($\omega_i = 0.15$, $\Delta AIC_c = 1.72$) but in both models the age parameter was not informative. The rest of the models were ≥ 8.08 ΔAIC_c from the top model.

Observed Shannon's diversity index (SHDI) values ranged from 0 (home range was only 1 habitat type) to 1.37 (all habitat types present in roughly equal proportions). Increasing SHDI by 0.5 correlated with an increase of 30.47% in home range size ($\beta = 0.53$, 95% CI = 0.29 –

0.77; Figure 7). Home range sizes decreased from 49.35 ha (95% CI = 28.87 ha – 84.34 ha) in week -3 to 17.72 ha (95% CI = 10.32 ha – 30.42 ha) in week 0 (β = -1.02, 95% CI = -1.15 – -0.90; Figure 5), as measured with the mean observed SHDI value. Home range sizes increased by 7.82% (β = -0.95, 95% CI = -1.08– -0.82) from week 0 to week 1, increased an additional 21.57% from week 1 to week 2 (β = -0.75, 95% CI = -0.89 – -0.62), and 8.42% from week 2 to week 3 (β = -0.67, 95% CI = -0.81 – -0.54). Home range sizes in week 3 were 95.94% smaller than in week -3 (Figure 8).

The distance between weekly home range centers was best explained by the week of parturition (ω_i = 0.42, ΔAIC_c = 0.62), the second most supported model in the set. The most supported model was week of parturition + age (ω_i = 0.57), but the additional age parameter was not informative (β = -0.22, 95% CI = -0.48 – 0.04). The rest of the models were ≥ 8.46 ΔAIC_c from the top model. The distance between the home range centers of week 0 and week -1 was 65.52% greater than the distance between the home range centers of week -1 and -2 (β = 0.72, 95% CI = 0.47 – 0.97; Figure 5). The distance between the home range centers of week 0 and week 1 was 38.06% smaller than the distance between weeks 0 and -1 (β = 0.40, 95% CI = 0.14 – 0.65). The distance between the centers of the other weeks were not different (week -3 vs. week -2: β = 0.10, 95% CI = -0.14 – 0.35; week -2 vs. week -1: β = 0.22, 95% CI = -0.02 – 0.47; week 1 vs. week 2: β = -0.01, 95% CI = -0.28 – 0.25).

Resource selection

Glaciated Plains – We modeled female resource selection based on 69,246 choice sets composed of 5 available locations and 1 used location, with 163 unique combinations of individual deer by period of parturition. The average radius of available habitat was 417.92 m.

We achieved convergence for all hyper-parameters in the model ($\hat{R} \leq 1.1$) and adequate goodness of fit for this model (Bayesian p-value = 0.37).

We found little evidence that females altered their resource selection before, during and after parturition, with the exception of the easterly aspect (Table 9, Figure 9). During parturition females were more likely to use 30-m X 30-m cells on the landscape that were east facing than west facing, whereas before and after parturition females exhibited no relationship between the probability of cell use and easterly aspect (Table 9, Figure 9). During all 3 parturition periods females exhibited a relatively high probability of using habitat classified as CRP and forest, with a lower probability of using crop, woody wetlands, and other habitat types (Table 9, Figure 10). Before parturition females were more likely to use CRP habitat than grassland habitat, but this relationship became less defined during and after parturition (Figure 10). Females were consistently more likely to use cells with a high percent canopy cover (Figure 11a), closer to wooded edges (Figure 11b), closer to roads (Figure 11c), and low slopes (Figure 11d) during all 3 parturition periods. Females were also consistently more likely to use cells that had a low road density (Figure 12a), and were south facing rather than north facing (Figure 12b) before, during and after parturition, but showed no relationship between probability of cell use and contagion during any parturition period (Table 9).

Ozarks – We modeled female deer resource selection based on 82,943 choice sets composed of 5 available locations and 1 used location, with 204 unique combinations of individual deer by period of parturition. The average radius of available habitat was 399.71 m. We achieved convergence for all hyper-parameters in the model ($\hat{R} \leq 1.1$) and adequate goodness of fit for this model (Bayesian p-value = 0.38).

We again found little evidence that females altered their resource selection before, during, and after parturition with the exception of the northerly aspect (Table 10). During and after parturition females were more likely to use 30-m X 30-m cells on the landscape that were south facing compared to north facing, whereas before parturition females exhibited no relationship between the probability of cell use and northerly aspect (Table 10, Figure 13). During all 3 parturition periods females exhibited a relatively high probability of using habitat classified as grassland and deciduous forest, with a lower probability of using evergreen forest (Table 10, Figure 14a). Before parturition females were more likely to use deciduous forest habitat than woody wetland habitat, but this relationship became less defined during and after parturition (Figure 14a). Females showed no preference or avoidance of cells that were categorized by mixed forest, evergreen forest, or other habitat categories. Females were consistently more likely to use cells that were categorized by low slopes (Figure 14b), and closer to wooded edges (Figure 14c) during all 3 parturition periods. The relative probability of a deer using a cell slightly increased before and after parturition as road density decreased (Figure 14d), but the 95% credible intervals for these time periods contained 0 (Table 10). Deer showed no relationship between probability of cell use and contagion, easterly aspect, canopy cover, and distance to nearest road (Table 10).

DISCUSSION

Contrary to our predictions, differences in predator species, land use, habitat types, and levels of fragmentation did not impact how pregnant female white-tailed deer altered their movement speeds and space use before and during parturition. For the 3 weeks prior to parturition movement speeds remained constant in both the OZ and GP, while home range sizes slowly declined (Figures 2, 4, 6, 8). During the week of parturition crepuscular movement speeds were similar in the OZ and GP, as were home range sizes. Furthermore, home range sizes in both study areas declined by roughly 178% from week -3 to the week of parturition. Female deer in the GP and OZ have different movement patterns during other times of the year (C. Wright, unpublished data), and respond differently to other stressors, such as the rifle hunting season (C. Wright, Chapter 3). Therefore it is somewhat surprising that they had almost the same movement speeds, and home range sizes during the week of parturition, as well as similar pre-parturition patterns. It is possible that close to the time of parturition physiological cues exhibit more control over pregnant female deer movements than differences in landscapes, which would lead to similarity in pre-parturition movements in the two study areas. Unfortunately we did not have a large enough sample size of non-pregnant females to draw conclusions about how pregnancy specifically affected movements in either study area. Bertrand et al. (1996) found that pregnant female white-tailed deer had different movement patterns than non-pregnant females, while other studies have observed no difference (Ciuti et al. 2006, Bongi et al. 2008). However, these studies all pooled ≥ 6 weeks of movements to make these comparisons, which could have masked any fine scale changes in pregnant female movements close to parturition.

Parturient females in the GP and OZ had similar pre-parturition movement patterns, but these movements were dissimilar from other ungulate species. For example, we did not observe a spike in movements immediately before giving birth, as has been observed in elk (Vore and Schmidt 2001), moose (Testa et al. 2000, McGraw et al. 2014, Severud et al. 2015, McLaren et al. 2017), red deer ([*Cervus elaphus*]; Asher et al. 2014), and woodland caribou ([*Rangifer tarandus caribou*]: Nagy 2011), nor did we observe large shifts in space use between pre-parturition areas of use and parturition sites (about 2 – 4 km in Bowyer et al. 1999, Testa et al. 2000, McGraw et al. 2014, Severud et al. 2015). We did observe that the largest distance between home ranges over the 7 week period was between week -1 and the week of parturition (Figure 5), which could suggest that females shifted their space use to locate a suitable birth site. However, this distance was < 250 m in both the OZ and GP, indicating that females did not move large distances to give birth. It has been hypothesized that pregnant females make large movements prior to giving birth to locate a site that offers greater protection from predators or greater nutritional quality habitat than their pre-parturition habitat (Testa et al. 2000, McGraw et al. 2014). The lack of increased movement or space use shifts prior to parturition in our study could be due to a lack of habitat heterogeneity within the study areas; traveling 2 – 4 km might not improve the probability of locating a more suitable site, so females stayed within their known area of use. However, to our knowledge no study has shown that white-tailed deer moved > 2 km to locate a birth site. Therefore, it is also possible that we did not observe large movements because white-tailed deer are habitat generalists who do not have specific habitat requirements in which to give birth, unlike more specialized ungulates (i.e., moose). More fine scale movement data is needed during this time period for white-tailed deer to fully understand the relationship between habitat requirements and birth sites.

Contrary to their movements prior to giving birth, white-tailed deer in both study areas exhibited a reduction in movement during parturition that is consistent with other species (mule deer [*Odocoileus hemionus*]: Long et al. 2009; elk: Vore and Schmidt 2001, Brook 2010; woodland caribou: Nagy 2011, DeMars et al. 2013; moose: Severud et al. 2015, McLaren et al. 2017, red deer: Asher et al. 2014), as well as white-tailed deer in other regions (Connecticut, USA: Bertrand et al. 1996; South Carolina, USA: D’Angelo et al. 2004; Oklahoma, USA: Webb et al. 2010). This similarity despite differences in habitat types, predators, landscape features, and species, suggests that a reduction in space use and movements during parturition may be a general rule in ungulates. Reduced movements could be related to the physical birthing process (Bartush and Lewis 1978) and reduced neonate mobility (Lent 1974**)**. However we, and other studies, were able to observe localized movements for > 1 day, but ≤ 1 week following parturition (Poole et al. 2007, Long et al. 2009, Nagy 2011, Severud et al. 2015, Melin et al. 2016, McLaren et al. 2017), which would indicate that this reduction in movements is not solely due to birthing or neonate mobility. Reduced movements might be necessary to ensure proper mother-infant bonding (Ozoga et al. 1982, DeYoung and Miller 2011), which can be crucial for neonate survival (Cook et al. 1971, Ozoga et al. 1982). Additionally, localized movements could be an antipredator defense; Bowyer et al. (1999) hypothesized that moose remained near their birth site to minimize scent trails left by the dam, thus reducing the ability of a predator to locate the birth site and the neonate. However, it is also likely that the longer the dam-neonate pair remain at the birth site, the greater their chances of a predator encounter (McGraw et al. 2014).

Therefore, when and how dams begin increasing their movements post parturition could be more habitat, predator, and species specific than their parturition movements. We observed that females in the OZ increased their crepuscular movement speeds post-parturition more rapidly than in the GP, even though home range sizes in both areas remained small. White-tailed deer are most active during crepuscular hours (Beier and McCullough 1990, Webb et al. 2010), and this is likely when they spend most of their time foraging (Beier and McCullough 1990). Therefore, this increase in post-parturition movements could be related to forage depletion at the birth site in the OZ (McGraw et al. 2014). Females in the OZ do not have access to the nutrient dense crop and CRP fields that characterize the GP, so they may have had to increase their movements within their reduced home ranges more than females in the GP to acquire a similar amount of forage in their forested landscapes.

Contrary to our predictions, deer in both study areas exhibited constant patterns of resource selection before, during, and after parturition, with the exception of how they used east and south facing slopes. During parturition females in the GP were more likely to use slopes that were southeast facing than southwest facing, whereas before and after parturition they used south facing slopes with no preference for east or west. In the OZ females used south facing slopes more than north facing slopes during and after parturition, but showed no preference for any direction before parturition. Both of these shifts in use are likely related to thermoregulation; south facing slopes are typically warmer than north facing slopes because they receive more sunlight (Bowyer et al. 1999, Long et al. 2009, Barbknecht et al. 2011), and east facing slopes receive more morning sunlight than west facing slopes. Neonates are susceptible to hypothermia (Van Moorter et al. 2009, Grovenburg et al. 2012*a*), so dams in both areas may have selected for south facing sites during and after parturition because they offered greater amounts of thermal radiation from the sun during all times of the day (Huegel et al. 1985). The use of southeast facing slopes in the GP during parturition may be due to the large amounts of morning dew present on CRP grasses. Wet pelage can decrease body temperatures of neonates (Barrett 1981), thereby increasing energy expenditure (Parker and Robbins 1985, Mysterud and Ostbye 1999). Therefore, increasing the amount of sunlight received at locations in the morning may increase the rate of dew evaporation, and thus reduce the probability of neonates getting hypothermia and conserve more energy.

Neonate thermoregulation may also be one of the drivers behind dam selection for CRP fields in the GP during and after parturition; Grovenburg et al. (2012*a*) found that neonate bed site temperatures were greater in CRP fields than wheat fields, and all their observed hypothermia mortalities occurred in wheat fields. CRP is also good hiding cover for neonates from predators (Grovenburg et al. 2010, 2012*a*), as well as suitable forage for dams prior to parturition (Gould and Jenkins 1993, Grovenburg et al. 2011) which would explain their continuous selection of CRP from pre to post parturition. Despite soybean and corn crops being an important food source for deer in the GP (Nixon et al. 1991), females showed low probability of selection of crop fields during all 3 phases of parturition. Prior to parturition, crops were unlikely to be tall or dense enough to serve as cover habitat for dams (Kernohan 1994) or a source of substantial forage (Grovenburg et al. 2011), and following parturition they would have been poor cover habitat for neonates (Grovenburg et al. 2012*a*). It is possible that if we had examined doe resource selection later in the summer, when neonates were more mobile and crop plants taller and more nutritious, we would have seen a shift in use from CRP to crops (Grovenburg et al. 2011).

The habitat types available to females in the OZ were different than in the GP, but they likely made habitat selection choices based on similar functional attributes. Females in the OZ were more likely to use deciduous forest than mixed and evergreen forest during all 3 phases of parturition (Figure 14a). Deciduous forests in the Missouri Ozarks are typically characterized by diverse and dense understory plant communities, which would provide adequate forage for the dam prior to parturition (Vangilder et al. 1982, McCullough et al. 1985), and hiding cover for the neonate during and after parturition (Grovenburg et al. 2010, Pitman et al. 2014). Unfortunately we did not have fine scale vegetation data to determine if understory plant communities were less dense in mixed and evergreen forests than deciduous forests, which could explain why dams preferred deciduous forests. It is also possible that the low relative selection of mixed and evergreen forest was an artifact of low availability (Manly et al. 2002); these habitat types were the two of the least common habitats found within the OZ.

Parturient females in the GP and OZ both selected for areas that were closer to a wooded edge before, during, and after parturition. White-tailed deer are thought to prefer edge habitats because of the high diversity of browse and forbs within these areas (Stewart et al. 2011), which can provide high quality nutritional forage for dams during gestation and lactation (Rohm et al. 2007). However, Gates and Gysel (1978) proposed that predators view edges as better foraging opportunities because these areas tend to harbor greater prey densities, which would negatively impact neonate survival. We did not observe any relationship between edge density within the dam's home range and neonate survival in the OZ, but in the GP neonate survival decreased with increased edge density (C. Wright, chapter 1). This negative relationship makes the reasoning behind dam selection for areas closer to wooded edges less clear in the GP. Perhaps the presence of row crop agriculture has created harder edges (Schneider et al. 2012) than were present historically, which has led to an ecological trap in the GP; dams prefer edge habitat because of increased forage availability and diversity (Stewart et al. 2011), while the lack of escape cover on the crop side has led to increased neonate predation (Grovenburg et al. 2012*b*).

Coyotes, a large source of neonate mortality (Ballard 2011), tend to use easily traversable terrain over steep slopes (Fox and Krausman 1994, Arjo and Pletscher 2004). Some studies have shown that dams and their young use moderate to steep slopes during and after parturition (Fox and Krausman 1994, Long et al. 2009, Karsch et al. 2016), presumably to reduce the risk of predation. We therefore expected dams to select for steeper slopes during and after parturition, but actually observed consistent selection for gentle slopes in both study areas. This pattern of selection is less surprising in the GP because the area is characterized by low, rolling hills that may not impede predator movements even in the steepest of areas. However topography in the OZ is highly variable, and includes slopes from $0^{o} – 30^{o}$, which could influence coyote movements (Fox and Krausman 1994). It is possible that females selected for more gentle slopes because neonates can have trouble traversing steep slopes, which can lead to accidental falls (Bergerud et al. 1984, Nobert et al. 2016). Alternatively, dams may have selected for gentle slopes post parturition because they reduce the energetic costs of locomotion (Hewitt 2011) during the already metabolically expensive lactation period. Neonates select for their own bed sites within the dams home range (Ozoga et al. 1982, Schwede et al. 1993), so they may have selected for steeper slopes as an antipredator defense (Pitman et al. 2014), which we were unable to observe.

Overall, pregnant and lactating females in both study areas selected for sites with similar resource attributes, despite many differences between the 2 regions. Furthermore, females largely did not alter what resources they selected for before, during, and after parturition, unlike mule deer (Long et al. 2009), caribou (Barten et al. 2001, Nobert et al. 2016), fallow deer (Ciuti et al. 2006), elk (Pitman et al. 2014), and moose (Melin et al. 2016). There are a few plausible explanations for our results including the possibility that dams shifted their resource selection at a smaller spatio-temporal scale than we were able to measure. All of our resource attributes were remotely sensed within 30-m X 30-m cells, and we did not differentiate use by time of day. Our movement metrics showed that dams altered their crepuscular movements more than day or night movements in response to parturition, and thus changes in resource selection may also have been affected by time of day. However, the fact that we observed similarity in resource selection between the two study areas and a lack of shifts in resource selection suggests that our results could be related to the generalist nature of white-tailed deer. Females in our study areas might not have had to make trade-offs between acquiring adequate forage to sustain lactation and avoiding neonate predation because no trade-offs exist; areas suitable for neonates might also have adequate foraging opportunities for females. However, more fine scale movement and resource selection data are needed for white-tailed deer to further explore this hypothesis.

MANAGEMENT IMPLICATIONS

Despite a lack of apparent specialized requirements for white-tailed deer to birth and raise neonates, females consistently selected for CRP grasslands in the GP and forests in the OZ, suggesting that these habitats offer both adequate forage for dams and concealment for neonates. However, land enrolled in CRP has declined by 13.40 million acres since its peak in 2007 at 36.8 million acres (USDA 2017). This reduction is due in part to rising commodity prices and a reduced enrollment cap. Given the importance of CRP habitat to females during this metabolically expensive time period, we suggest that managers place an emphasis on maintaining current levels of CRP, or planting habitat with similar functional attributes. In more forested habitats, where enrolling land in CRP is not a feasible option, we recommend managing forest stands to have a dense understory to increase forage availability for dams and hiding and thermal cover for neonates.

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TABLES

Table 1. Set of candidate models used to determine what factors influence the movement speed (meters per hour) of female white-tailed deer before, during, and after parturition in the Glaciated Plains and Ozark Regions of Missouri, USA, 2015 – 2017.

Model[a,b]	K[c]
Null	4
Age	5
Time of Day	6
Forest	5
Week	10
Time of day × Forest	9
Time of day + Forest + Age	8
Time of day × Age	9
Time of day × Forest + Age	10
Week + Time of day + Forest + Age	14
Week × Time of day	24
Week × Time of day + Forest	25
Week × Time of day + Forest + Age	26
Time of day × Forest + Week	15
Time of day × Age + Week	15

[a] Age = adult or sub-adults, time of day = day, night or crepuscular, forest = forested or non-forested location, week = the 3 weeks before parturition, week of parturition and 3 weeks following parturition (7 weeks total).

[b] Unique deer identification and year were included as a random effects in all models.

[c] Number of parameters.

Table 2. Description of the most common land cover types found in the Glaciated Plains and Ozark regions of Missouri, USA 2015 – 2017. These cover types were used to calculate the Shannon’s diversity index of female white-tailed deer home ranges, and evaluate resource selection before, during, and after parturition.

Land cover type	Description
Grassland	Areas containing 20% or greater graminoid or herbaceous vegetation. Can be used for grazing or hay production.
Cultivated crop[a]	All land being tilled and/or used for the production of annual crops, such as corn and soybeans, and perennial woody crops. Crop vegetation constitutes > 20% of total vegetation.
Deciduous forest[b]	Areas where 75% of tree species > 5 m tall shed their leaves in the fall. Trees make up > 20% of the total vegetation.
Evergreen forest[b]	Areas where 75% of tree species > 5 m tall maintain their leaves all year. Trees make up > 20% of the total vegetation.
Mixed forest[b]	Areas where trees make up > 20% of the total vegetation, but neither deciduous nor evergreen trees make up 75% of the total tree cover.
Woody wetlands	Areas where the soil is periodically covered or saturated with water and shrubland vegetation makes up > 20% of the vegetation.
CRP[c]	Land enrolled in the conservation reserve program; typically comprised of native grasses and other native vegetation planted to improve wildlife habitat and prevent erosion.
Other	Habitat classes found in the study area that are not one of the above

	vegetation classes.

[a] Included in other category for resource selection analysis conducted in the Ozark region.

[b] Combined into 1 forest category for resource selection analysis conduction the Glaciated Plains region.

[c] Land enrolled in the conservation reserve program. Not present in the Ozark region.

Table 3. Set of candidate models used to determine what factors most influence the area (ha) of female white-tailed deer space use before, during and after parturition in the Glaciated Plains and Ozark Regions of Missouri, USA, 2015 – 2017.

Model[a,b]	K[c]
Null	4
Age	5
Forest	5
Age + Forest	6
Age × Forest	7
Week	10
Week + Age + Forest	12
Week × Age	17
Week + Age	11
Week × Age + Forest	18
Week + Forest	11
Week × Forest	17
Week × Forest + Age	18
Age × Forest + Week	13
Week + Age + Diversity	12
Week × Age + Diversity	18
Week × Diversity + Age	18
Week × Diversity	17
Week + Diversity	11

[a] Age = adult or sub-adult, forest = proportion of home range forested, diversity = measure of patch diversity using Shannon's diversity index, week = the 3 weeks before parturition, week of parturition and 3 weeks following parturition (7 weeks total).

[b] Deer identification and year were included as a random effects in all models.

[c] Number of parameters.

Table 4. Description of the 9 resource attributes assigned to each used and available location included in the resource selection analysis conducted for female white-tailed deer before, during and after parturition in the Glaciated Plains (GP) and Ozark (OZ) regions of Missouri, USA, 2015 – 2017.

Covariate	Definition or measurement
Land cover type	6 vegetation classes - see table 2
% Canopy cover	0-100%; proportion of 30m cell covered with tree canopy
Distance to edge	Distance (m) from the location to the nearest edge - Distinct transition from a forest to an open area (grassland, cultivated crop, shrub/scrub)
Distance to road	Distance (m) from location to the nearest road
Road density[a]	Length of public roads (m) within a radius of 417.92 m (GP) or 399.71 m (OZ) from the location
Slope	From 0^o (flat) to 45^o
Aspect - north	From -1 (due south) to 1 (due north)
Aspect - east	From -1 (due west) to 1 (due east)
Contagion	Measures the degree to which patch types are aggregated or clumped together; from 0 (every cell is a different patch type) to 100 (landscape consists of a single patch)

[a] The radius used in each study area was the mean radius of available habitat for all used locations.

Table 5. Summary of female white-tailed deer pregnancy results in the Glaciated Plains (GP) and Ozark (OZ) eco-regions of Missouri, USA, 2015 – 2017. Pregnancy was determined using pregnancy specific protein B (PSPB) levels in the blood.

		2015		2016		2017	
Study Area	Age[a]	Pregnant	Not pregnant	Pregnant	Not pregnant	Pregnant	Not pregnant
GP	Fawn	3	14	1	15	4	11
	Yearling	2	0	4	0	8	0
	Adult	12	0	18	0	32	1
OZ	Fawn	2	11	1	28	4	33
	Yearling	5	0	6	1	27	1
	Adult	20	0	41	1	41	1

[a] Fawn: <1 year old at the start of the analysis, Yearling: < 2 years old at the start of the analysis, Adult: ≥ 2 years old at the start of the analysis

Table 6. Summary of female white-tailed deer included in movement, space use, and resource selection analyses before, during, and after parturition in the Glaciated Plains and Ozark eco-regions of Missouri, USA, 2015 – 2017.

Study Area	Age[a]	2015	2016	2017
Glaciated Plains	Fawn	3	1	1
	Yearling	2	9	1
	Adult	11	24	30
Ozarks	Fawn	1	0	2
	Yearling	5	3	4
	Adult	18	35	26

[a] Fawn: <1 year old at the start of the analysis, Yearling: < 2 years old at the start of the analysis, Adult: ≥ 2 years old at the start of the analysis

Table 7. Parameter estimates and 95% confidence intervals for the model week × time of day + forest, which was the top model explaining female white-tailed deer movement speeds before, during, and after parturition in the Glaciated Plains region of Missouri, USA 2015 – 2017. Parameter estimates and confidence intervals are on the log scale.

		95% Confidence Interval (CI)	
Parameter[a]	Estimate	Lower CI	Upper CI
Intercept	4.15	4.03	4.27
Week -3	0.22	0.13	0.30
Week -2	0.27	0.19	0.35
Week -1	0.24	0.16	0.32
Week 0	-0.16	-0.24	-0.07
Week 1	-0.11	-0.20	-0.03
Week 2	-0.05	-0.14	0.03
Day	-0.32	-0.40	-0.25
Night	-0.36	-0.45	-0.28
Forested	-0.07	-0.09	-0.05
Week -3 × Day	-0.49	-0.59	-0.39
Week -2 × Day	-0.57	-0.66	-0.47
Week -1 × Day	-0.55	-0.65	-0.46
Week 0 × Day	0.02	-0.08	0.12
Week 1 × Day	0.01	-0.09	0.11
Week 2 × Day	0.00	-0.10	0.10
Week -3 × Night	-0.49	-0.61	-0.38

Week -2 × Night	-0.56	-0.67	-0.46
Week -1 × Night	-0.58	-0.68	-0.47
Week 0 × Night	-0.05	-0.16	0.06
Week 1 × Night	0.08	-0.04	0.19
Week 2 × Night	0.10	-0.02	0.21

[a] Variable notation: Weeks -3 – -1 are the 3 weeks prior to parturition, week 0 is the week of parturition and weeks 1 – 2 are the 2 weeks post parturition. The intercept term includes week 3 during crepuscular hours.

Table 8. Parameter estimates and 95% confidence intervals for the model week × time of day + forest, which was the top model explaining female white-tailed deer movement speeds before, during, and after parturition in the Ozark region of Missouri, USA 2015 – 2017. Parameter estimates and confidence intervals are on the log scale.

		95% Confidence Interval (CI)	
Parameter[a]	Estimate	Lower CI	Upper CI
Intercept	4.16	4.08	4.24
Week -3	-0.03	-0.11	0.05
Week -2	0.01	-0.07	0.09
Week -1	-0.01	-0.08	0.06
Week 0	-0.28	-0.35	-0.20
Week 1	-0.16	-0.24	-0.08
Week 2	-0.01	-0.09	0.07
Day	-0.30	-0.37	-0.24
Night	-0.28	-0.35	-0.21
Forested	0.06	0.04	0.08
Week -3 × Day	-0.11	-0.20	-0.02
Week -2 × Day	-0.16	-0.25	-0.07
Week -1 × Day	-0.19	-0.28	-0.11
Week 0 × Day	0.21	0.12	0.29
Week 1 × Day	0.15	0.06	0.23
Week 2 × Day	0.04	-0.06	0.13
Week -3 × Night	-0.32	-0.42	-0.21

Week -2 × Night	-0.43	-0.52	-0.33
Week -1 × Night	-0.45	-0.54	-0.36
Week 0 × Night	-0.05	-0.15	0.04
Week 1 × Night	-0.03	-0.12	0.07
Week 2 × Night	-0.04	-0.14	0.06

[a] Variable notation: Weeks -3 – -1 are the 3 weeks prior to parturition, week 0 is the week of parturition and weeks 1 – 2 are the 2 weeks post parturition. The intercept term includes week 3 during crepuscular hours.

Table 9. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the discrete choice resource selection model for female white-tailed deer before, during, and after parturition in the Glaciated Plains region of Missouri, USA, 2015 – 2017. For each variable [1] represents the intercept (before parturition), [2] the additive effect during parturition, and [3] the additive effect after parturition.

			95% Credible Interval (CrI)	
Variable	Mean	SD	Lower CrI	Upper CrI
Forest [1]	0.69	0.08	0.53	0.85
Forest [2]	0.05	0.11	-0.16	0.26
Forest [3]	0.15	0.12	-0.09	0.39
Grassland [1]	0.31	0.09	0.12	0.50
Grassland [2]	0.10	0.12	-0.14	0.35
Grassland [3]	-0.02	0.14	-0.30	0.24
CRP[a] [1]	0.87	0.10	0.67	1.07
CRP[a] [2]	0.19	0.13	-0.07	0.45
CRP[a] [3]	0.02	0.15	-0.27	0.31
Crop [1]	-0.16	0.11	-0.37	0.04
Crop [2]	0.15	0.14	-0.13	0.43
Crop [3]	-0.09	0.15	-0.39	0.21
Woody Wetlands [1]	-0.09	0.23	-0.57	0.34
Woody Wetlands [2]	0.09	0.28	-0.46	0.63
Woody Wetlands [3]	0.35	0.31	-0.26	0.97
Road density [1]	-0.73	0.19	-1.10	-0.36

Road density [2]	0.09	0.25	-0.39	0.58
Road density [3]	0.23	0.26	-0.27	0.73
Distance to road [1]	-0.32	0.09	-0.50	-0.14
Distance to road [2]	0.01	0.12	-0.23	0.25
Distance to road [3]	0.22	0.13	-0.02	0.47
Distance to edge [1]	-0.29	0.05	-0.39	-0.20
Distance to edge [2]	0.02	0.07	-0.11	0.15
Distance to edge [3]	0.01	0.07	-0.13	0.15
Canopy cover [1]	0.41	0.04	0.33	0.48
Canopy cover [2]	0.05	0.05	-0.05	0.15
Canopy cover [3]	0.05	0.05	-0.05	0.16
Contagion [1]	-0.01	0.06	-0.12	0.10
Contagion [2]	0.01	0.08	-0.14	0.16
Contagion [3]	0.05	0.08	-0.11	0.21
Slope [1]	-0.15	0.03	-0.22	-0.08
Slope [2]	0.06	0.05	-0.03	0.15
Slope [3]	0.00	0.05	-0.10	0.09
North [1]	-0.09	0.03	-0.14	-0.03
North [2]	0.03	0.04	-0.04	0.11
North [3]	-0.03	0.04	-0.11	0.05
East [1]	0.08	0.03	0.01	0.14
East [2]	-0.12	0.04	-0.21	-0.03
East [3]	0.12	0.05	0.03	0.21

[a] CRP = grasses enrolled in the conservation reserve program

Table 10. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the discrete choice resource selection model for female white-tailed deer before, during, and after parturition in the Ozark region of Missouri, USA, 2015 – 2017. For each variable [1] represents the intercept (before parturition), [2] the additive effect during parturition, and [3] the additive effect after parturition.

			95% Credible Interval (CrI)	
Variable	Mean	SD	Lower CrI	Upper CrI
Mixed forest [1]	-0.09	0.13	-0.37	0.16
Mixed forest [2]	-0.16	0.15	-0.46	0.14
Mixed forest [3]	0.19	0.18	-0.16	0.54
Grassland [1]	0.30	0.07	0.17	0.44
Grassland [2]	-0.09	0.09	-0.27	0.09
Grassland [3]	-0.01	0.10	-0.21	0.19
Deciduous forest [1]	0.48	0.06	0.37	0.60
Deciduous forest [2]	-0.14	0.07	-0.28	0.01
Deciduous forest [3]	0.12	0.08	-0.05	0.28
Evergreen forest [1]	-0.18	0.13	-0.45	0.06
Evergreen forest [2]	-0.19	0.15	-0.50	0.11
Evergreen forest [3]	0.05	0.18	-0.30	0.40
Woody wetlands [1]	-0.75	0.41	-1.62	-0.01
Woody wetlands [2]	-0.85	0.46	-1.77	0.05
Woody wetlands [3]	0.23	0.53	-0.83	1.27
Road density [1]	-0.24	0.12	-0.48	0.00

Road density [2]	-0.27	0.17	-0.60	0.07
Road density [3]	0.34	0.18	0.00	0.68
Distance to road [1]	-0.03	0.13	-0.28	0.22
Distance to road [2]	0.07	0.17	-0.26	0.41
Distance to road [3]	0.08	0.18	-0.26	0.43
Distance to edge [1]	-0.43	0.06	-0.56	-0.30
Distance to edge [2]	0.06	0.09	-0.12	0.24
Distance to edge [3]	-0.07	0.09	-0.25	0.11
Canopy cover [1]	0.01	0.04	-0.06	0.08
Canopy cover [2]	0.02	0.05	-0.08	0.12
Canopy cover [3]	0.03	0.05	-0.07	0.13
Contagion [1]	-0.06	0.06	-0.17	0.05
Contagion [2]	0.11	0.08	-0.04	0.27
Contagion [3]	0.04	0.08	-0.12	0.20
Slope [1]	-0.11	0.04	-0.19	-0.04
Slope [2]	0.04	0.05	-0.06	0.15
Slope [3]	-0.01	0.05	-0.12	0.09
North [1]	-0.06	0.03	-0.11	-0.01
North [2]	0.08	0.03	0.01	0.15
North [3]	-0.03	0.04	-0.10	0.04
East [1]	-0.04	0.03	-0.10	0.02
East [2]	0.00	0.04	-0.09	0.08
East [3]	0.00	0.04	-0.08	0.08

FIGURES

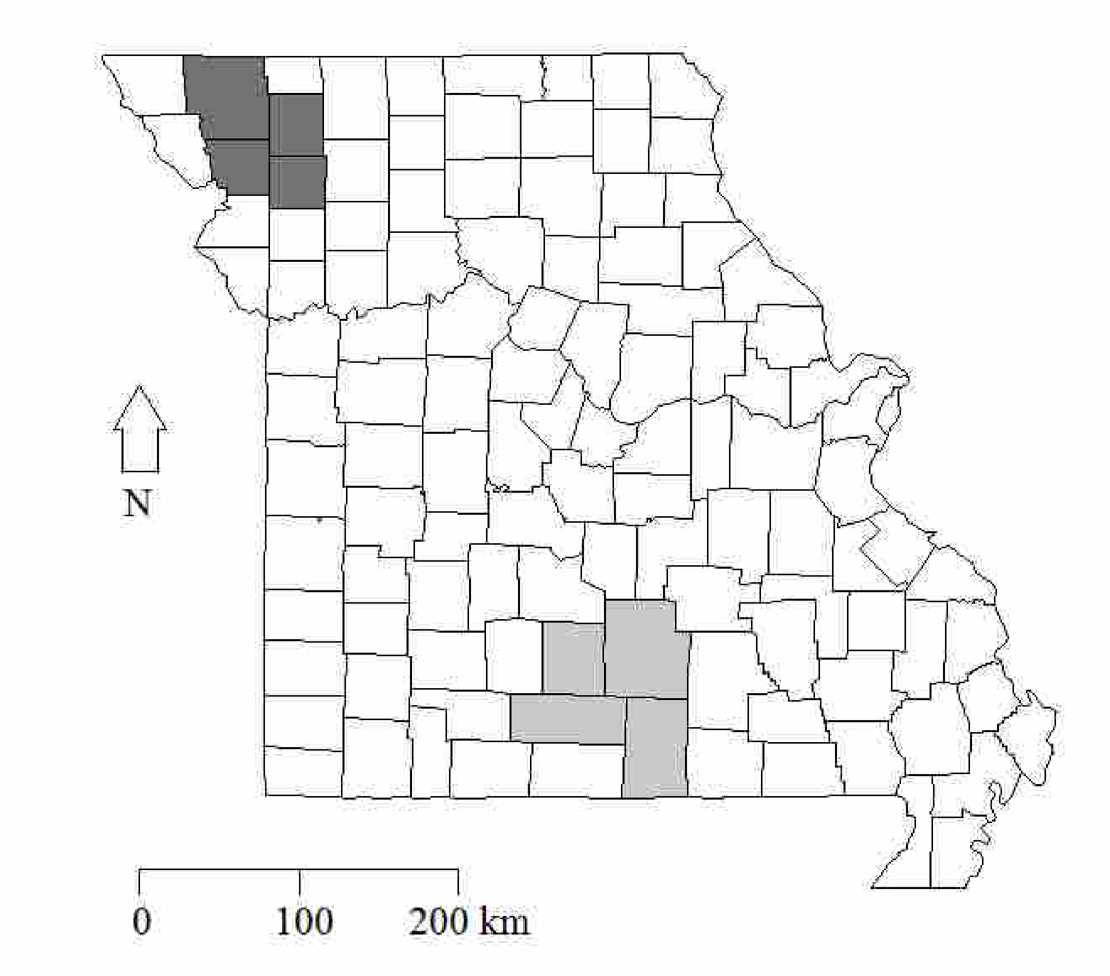

Figure 1. Map of the two study areas in Missouri, USA. The Glaciated Plains study area is shaded in dark grey and the Ozark study area is shaded in light grey.

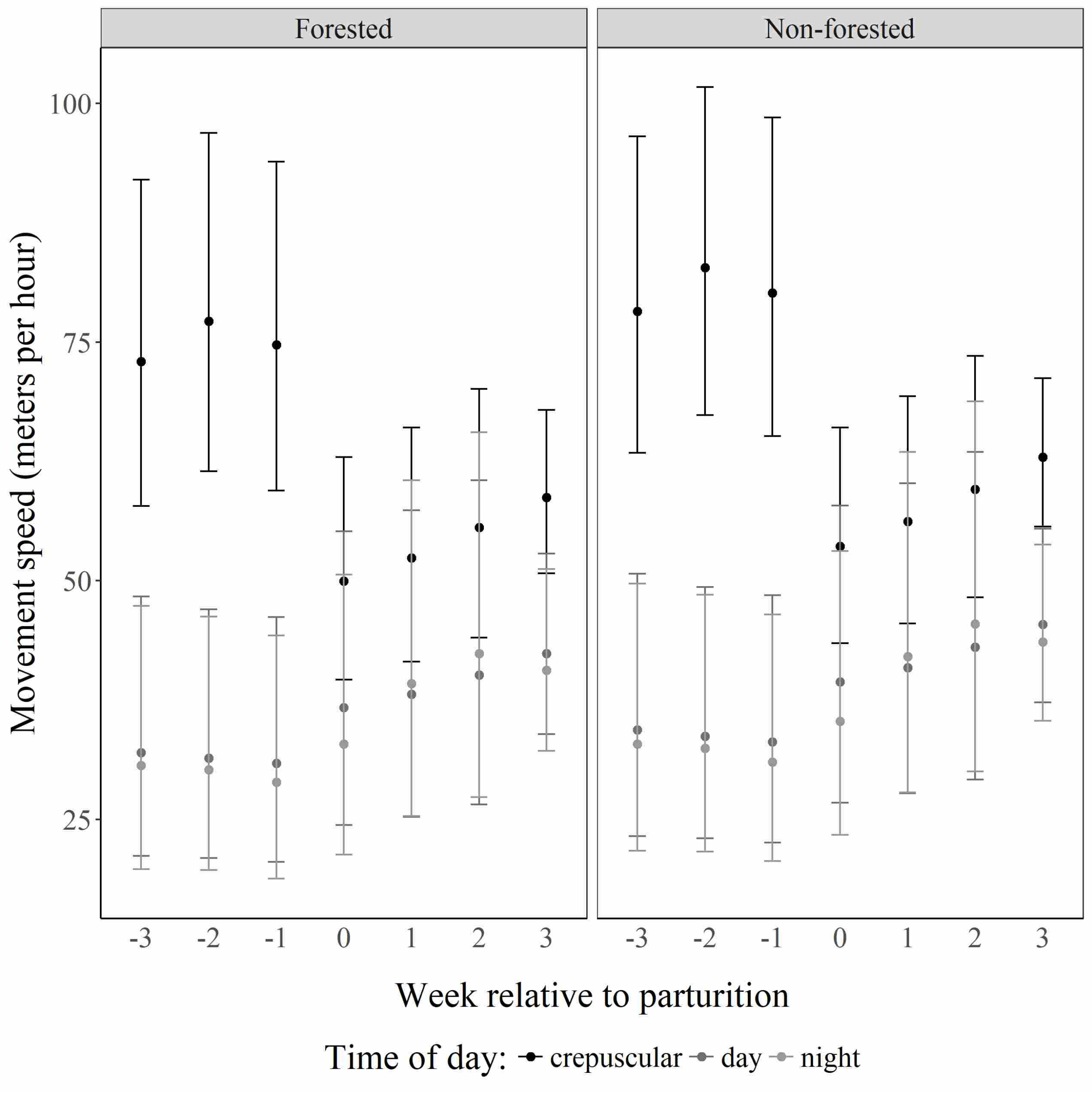

Figure 2. Fitted estimates of female white-tailed deer movement speeds before (weeks -3 through -1) and after parturition (weeks 1 – 3) in the Glaciated Plains region of Missouri, USA, 2015 – 2017. Estimates were obtained using the most supported model, time of day × week + forest, as determined by model selection. Error bars show the 95% confidence interval.

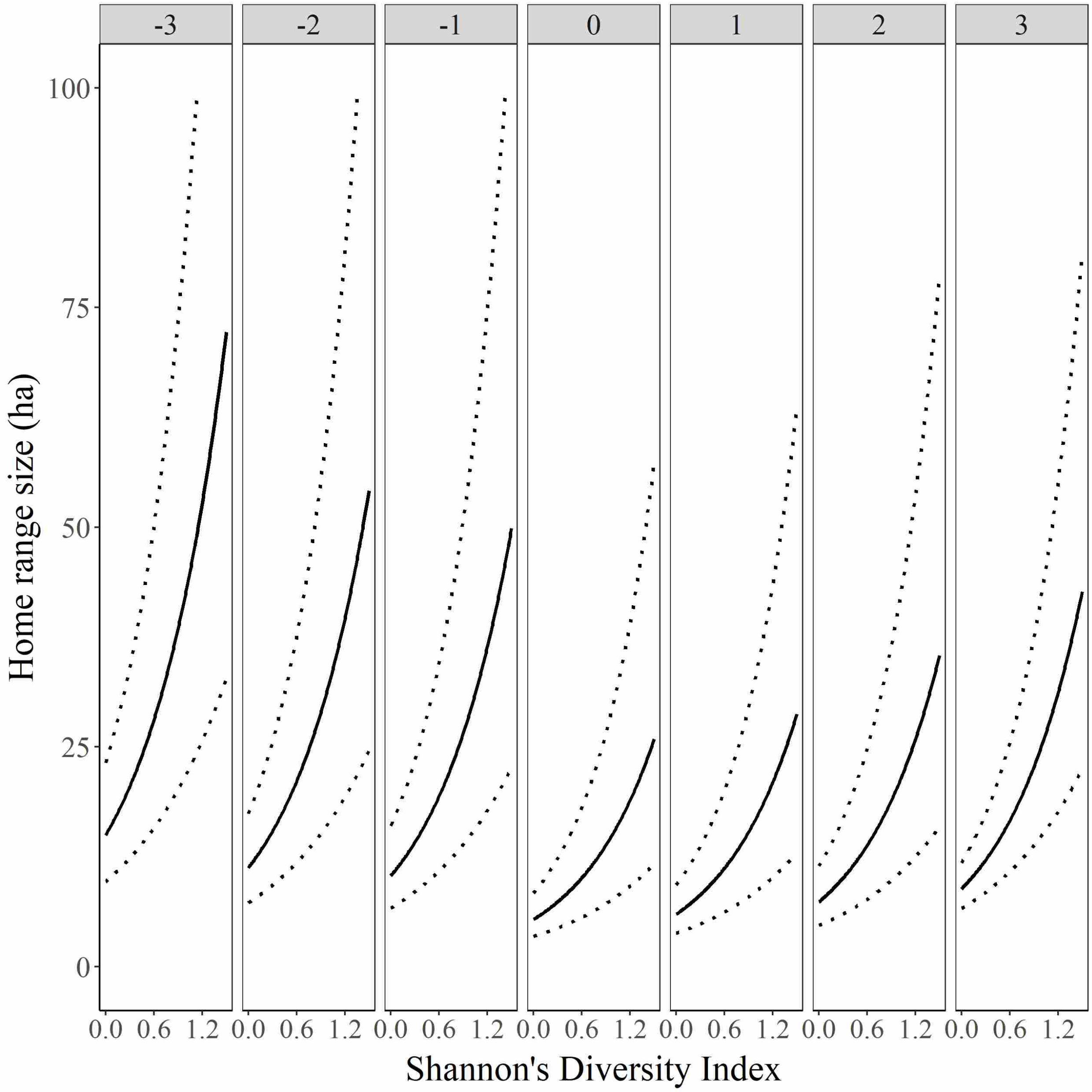

Figure 3. Fitted estimates of female white-tailed deer home range sizes before (weeks -3 through -1), during (week 0) and after parturition (weeks 1 – 3) in the Glaciated Plains region of Missouri, USA, 2015 – 2017. Estimates were obtained using the most supported model, week of parturition + Shannon's diversity index, as determined by model selection. Dashed lines show the 95% confidence interval.

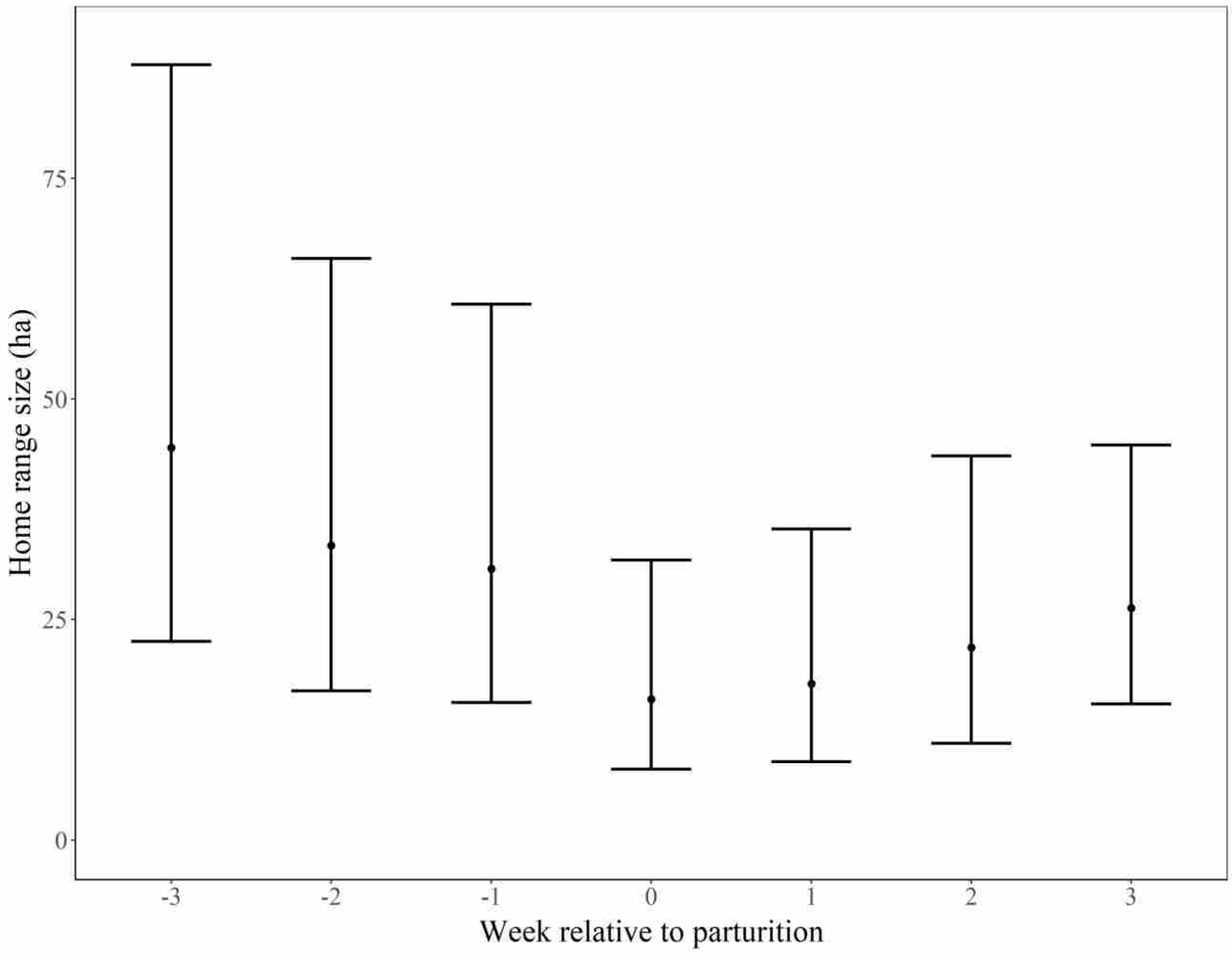

Figure 4. Fitted estimates of female white-tailed deer home range sizes before (weeks -3 through -1) and after parturition (weeks 1 – 3) in the Glaciated Plains region of Missouri, USA, 2015 – 2017. Estimates were obtained using the most supported model, week of parturition + Shannon's diversity index (SHDI), as determined by model selection. Error bars show the 95% confidence interval. We used the mean SHDI value observed (1.04) for all estimates of home range size to show effect sizes of week of parturition.

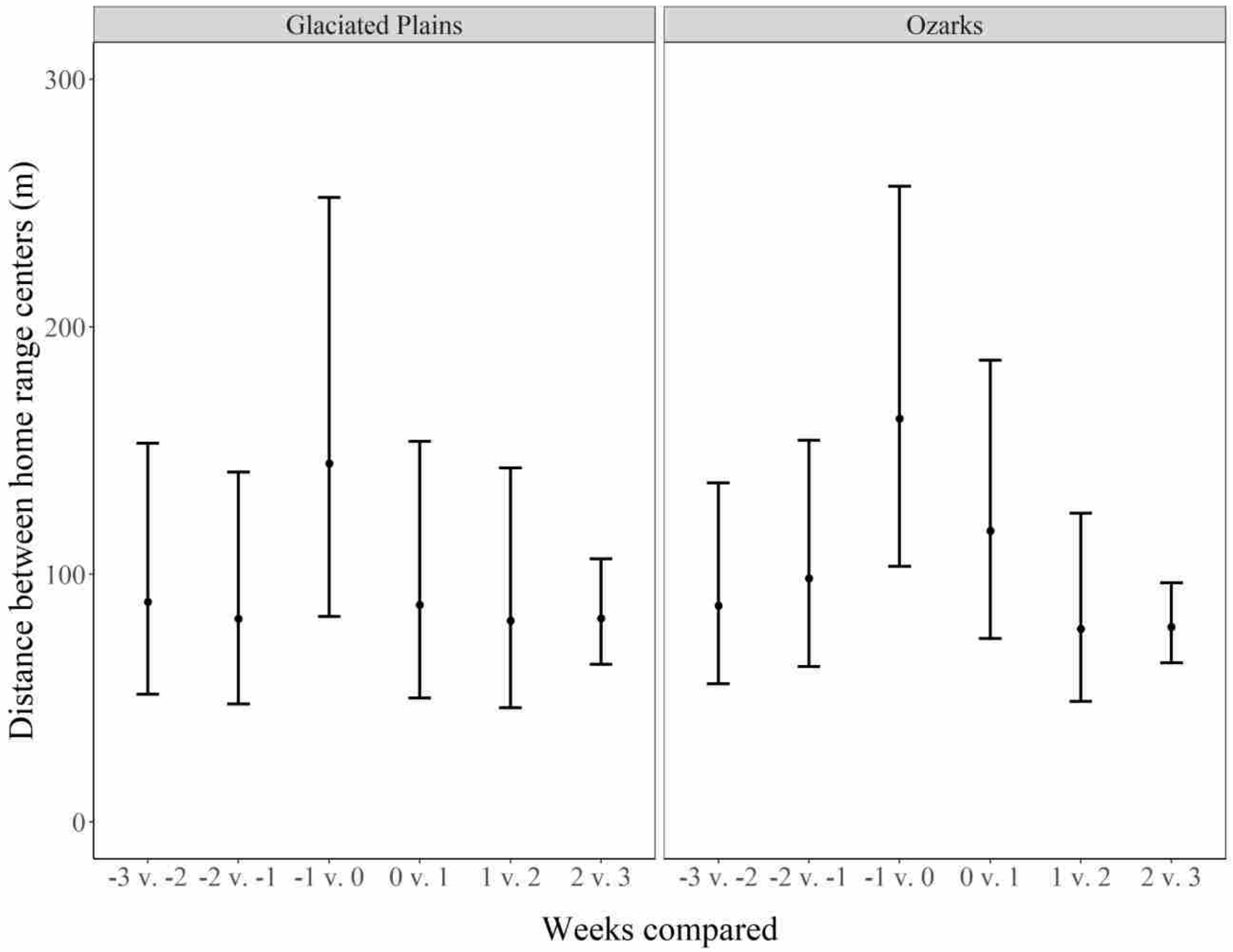

Figure 5. Fitted estimates of distances between centers of weekly home ranges for female white-tailed deer before (-3 to -1), during (0), and after (1 to 3) parturition in the Glaciated Plains and Ozark regions of Missouri, USA, 2015 – 2017. Distances between centers were calculated for successive weeks, so -3 vs. -2 is the distance between the center of a female's home range the third week before parturition and the second week before parturition. Estimates were obtained from the most supported model in each study area, as determined by model selection; error bars show the 95% confidence interval.

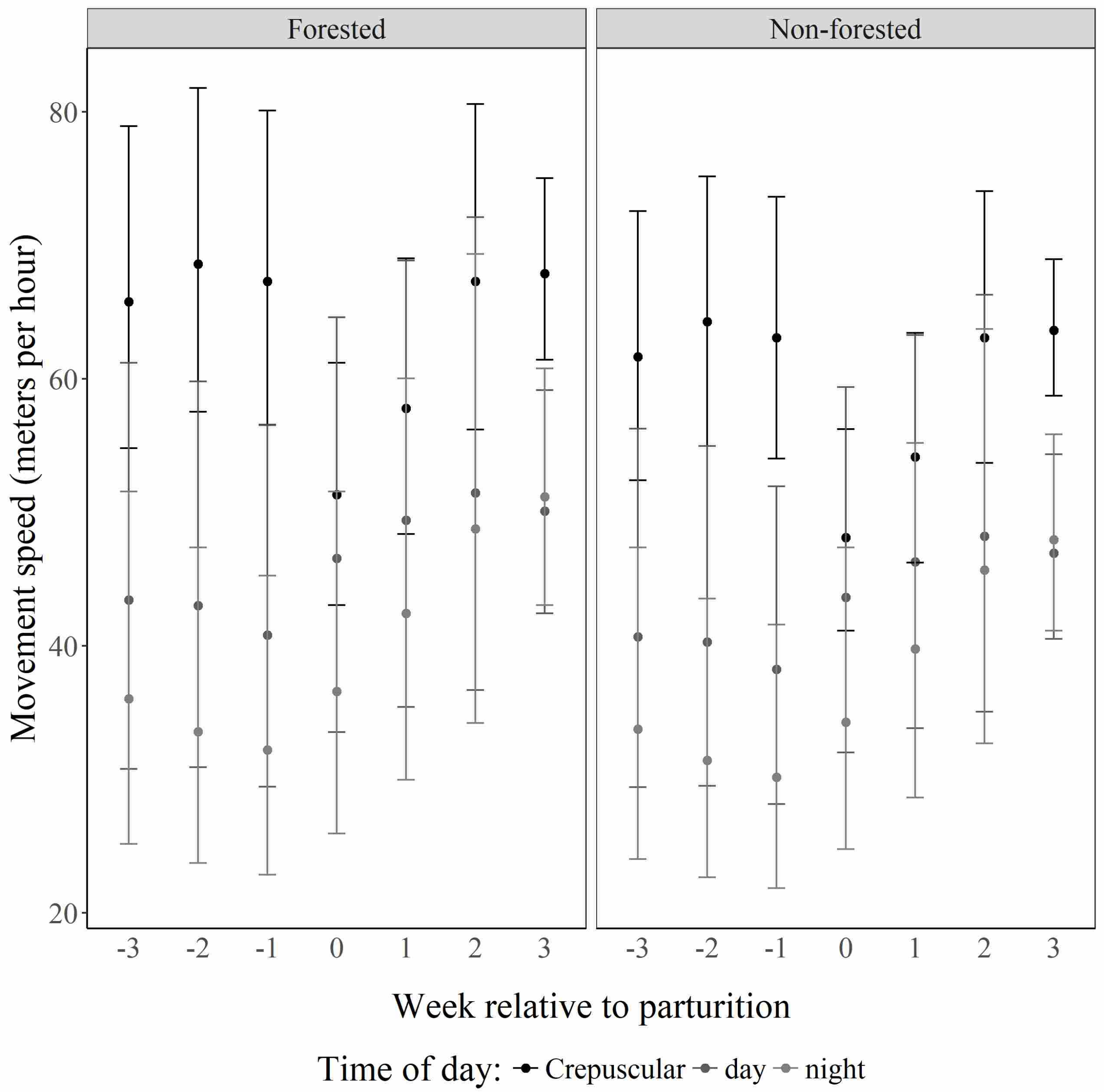

Figure 6. Fitted estimates of female white-tailed deer movement speeds before (weeks -3 through -1), during (week 0), and after parturition (weeks 1 – 3) in the Ozark study region, Missouri, USA, 2015 – 2017. Estimates were obtained using the most supported model, time of day × week + forest, as determined by model selection. Error bars show the 95% confidence interval.

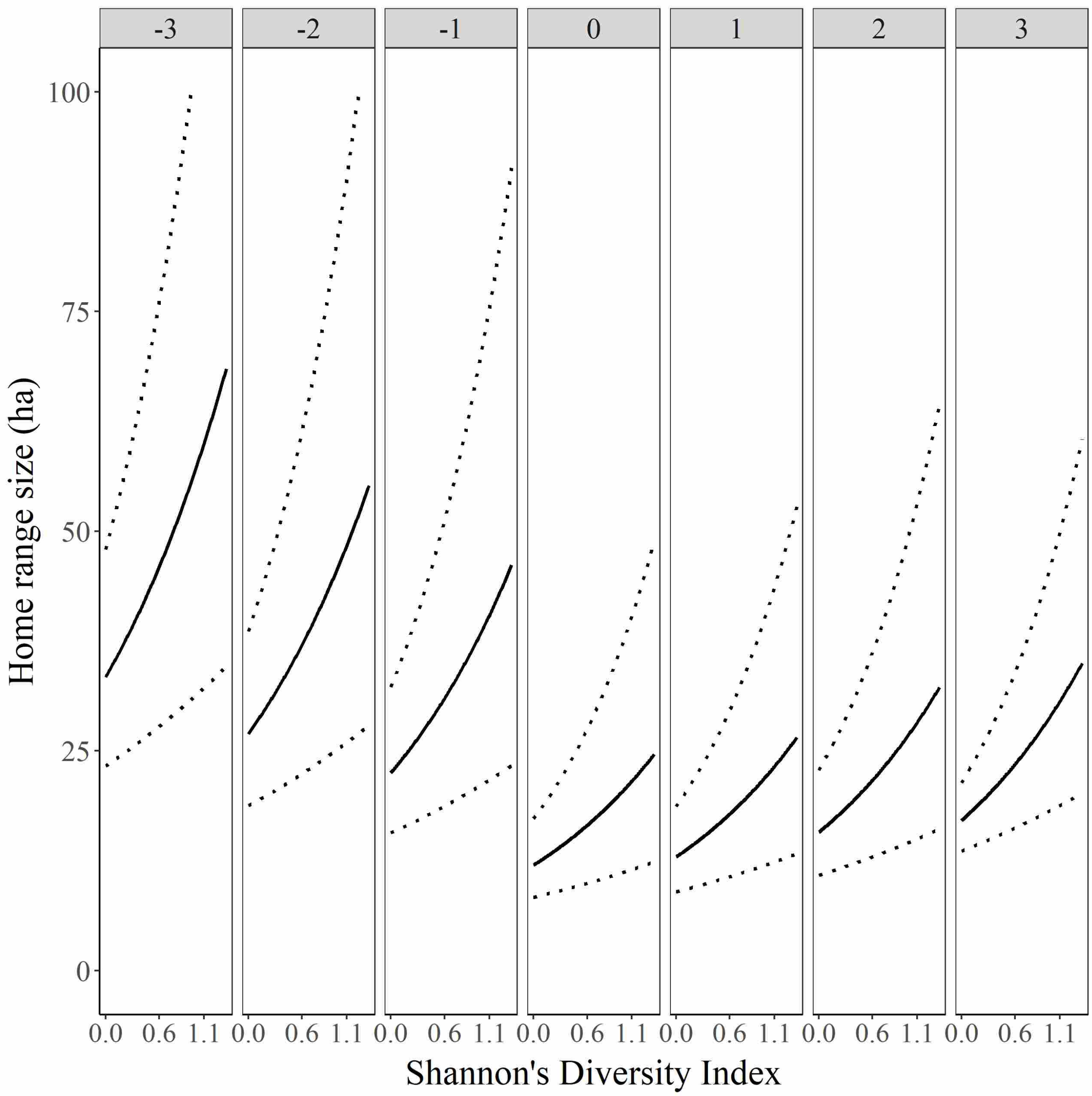

Figure 7. Fitted estimates of female white-tailed deer home range sizes before (weeks -3 through -1) and after parturition (weeks 1 – 3) in the Ozark study region, Missouri, USA, 2015 – 2017. Estimates were obtained using the most supported model, week of parturition + Shannon's diversity index, as determined by model selection. Dashed lines show 95% confidence intervals.

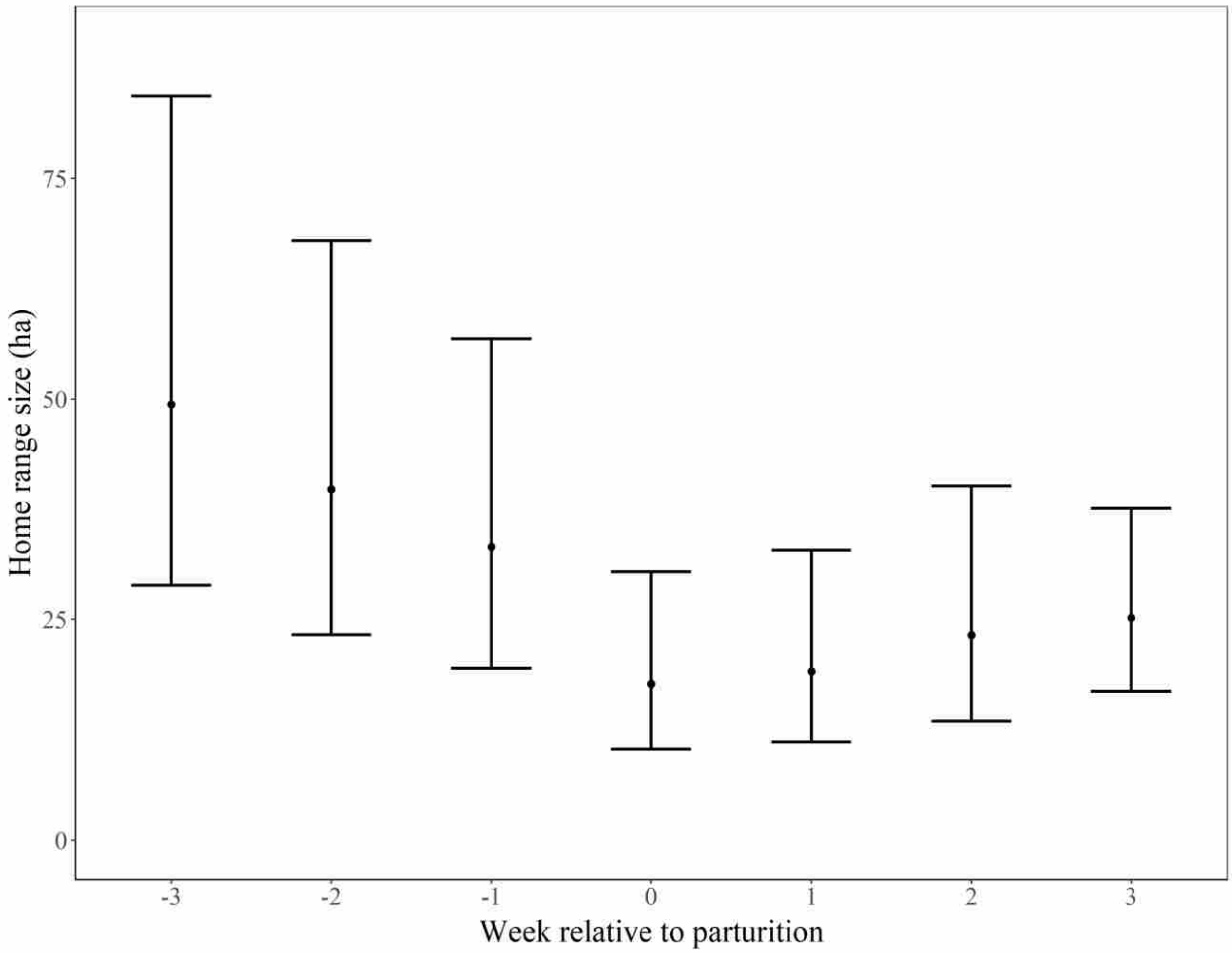

Figure 8. Fitted estimates of female white-tailed deer home range sizes before (weeks -3 through -1) , during (week 0), and after parturition (weeks 1 – 3) in the Ozark study region, Missouri, USA, 2015 – 2017. Estimates were obtained using the most supported model, week of parturition + Shannon’s diversity index (SHDI), as determined by model selection. Error bars show 95% confidence intervals. We used the mean SHDI value observed (0.73) for all estimates of home range size to show effect sizes of week of parturition.

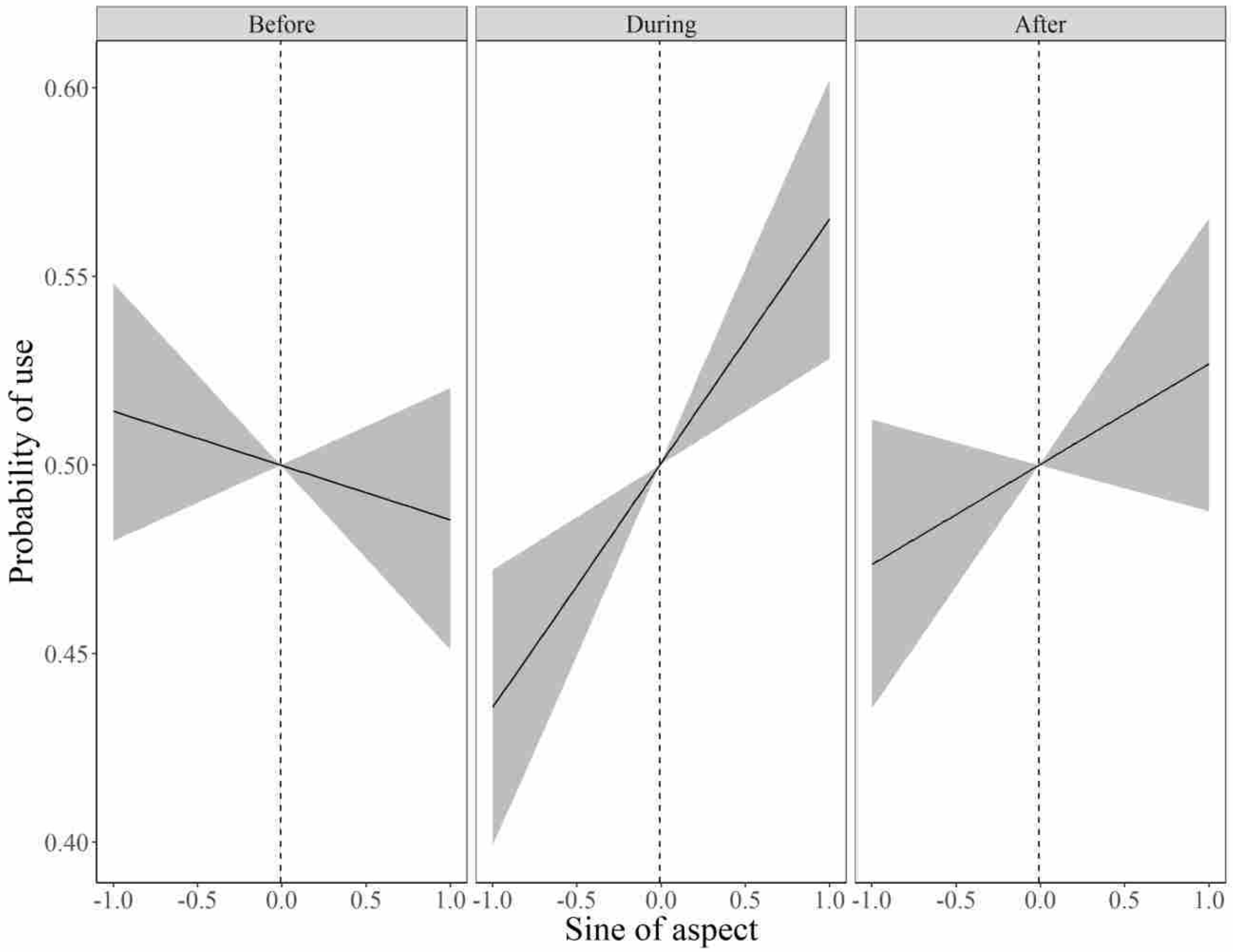

Figure 9. The probability of a female white-tailed deer in the Glaciated Plains region of Missouri, USA using a 30-m X 30-m cell as a function of the sine of the aspect (easterly aspect) before, during, and after parturition. Each panel assumes the deer is faced with 2 choices: the mean easterly aspect, represented by the dashed vertical line, or an alternative value that varies along the x-axis. All other variables are assumed constant and fixed at their mean observed value. Black lines represent the mean posterior distribution and gray ribbons represent the 95% credible interval.

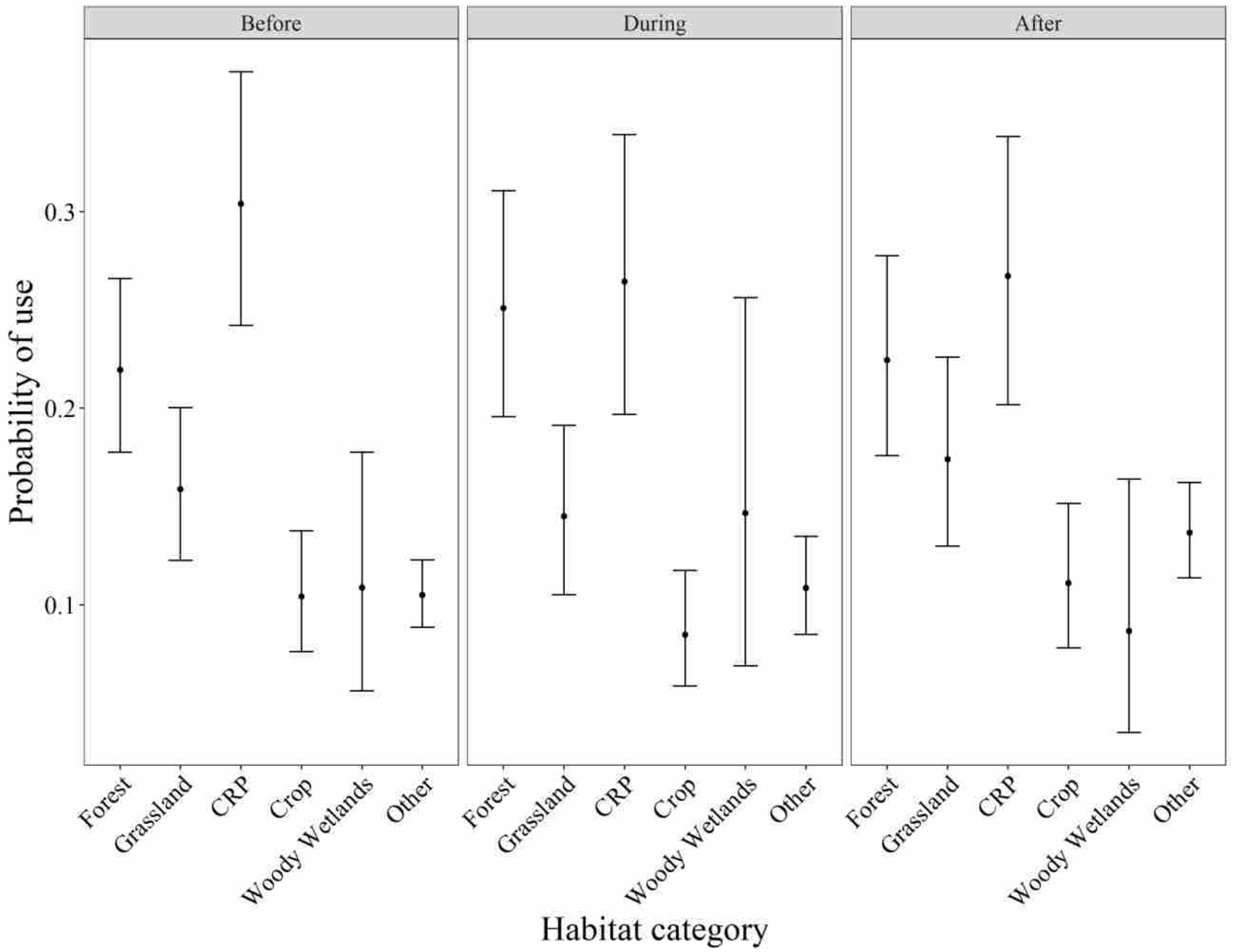

Figure 10. The probability of female white-tailed deer using a particular habitat category before, during, and after parturition in the Glaciated Plains region of Missouri, USA 2015 – 2017. Each panel assumes a deer is faced with 6 mututally exclusive alternatives to choose from. Circles represent the mean posterior distribution and error bars represent the 95% credible interval.

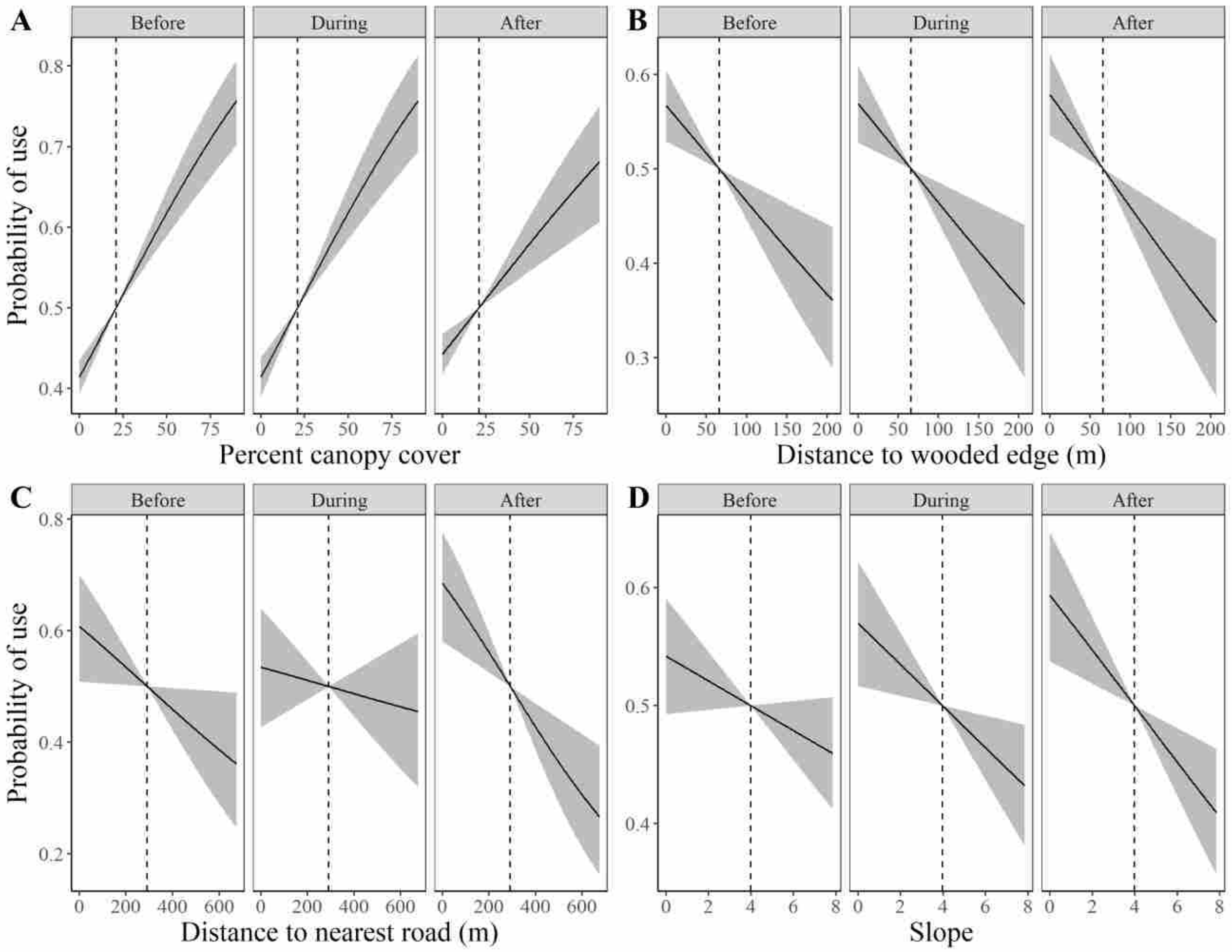

Figure 11. The probability of female white-tailed deer using a 30-m X 30-m cell before, during and after parturition as a function of A) Percent canopy cover, B) Distance to wooded edge, C) Distance to nearest road, and D) Slope, in the Glaciated Plains region of Missouri, USA, 2015 – 2017. Each panel assumes a female deer is faced with 2 alternatives: the value of the covariate at the observed mean value (represented by the dashed vertical line) or an alternative value that varies along the x-axis. All other variables are assumed constant and fixed at their mean observed value. Black lines represent the mean posterior distribution and gray ribbons represent the 95% credible interval.

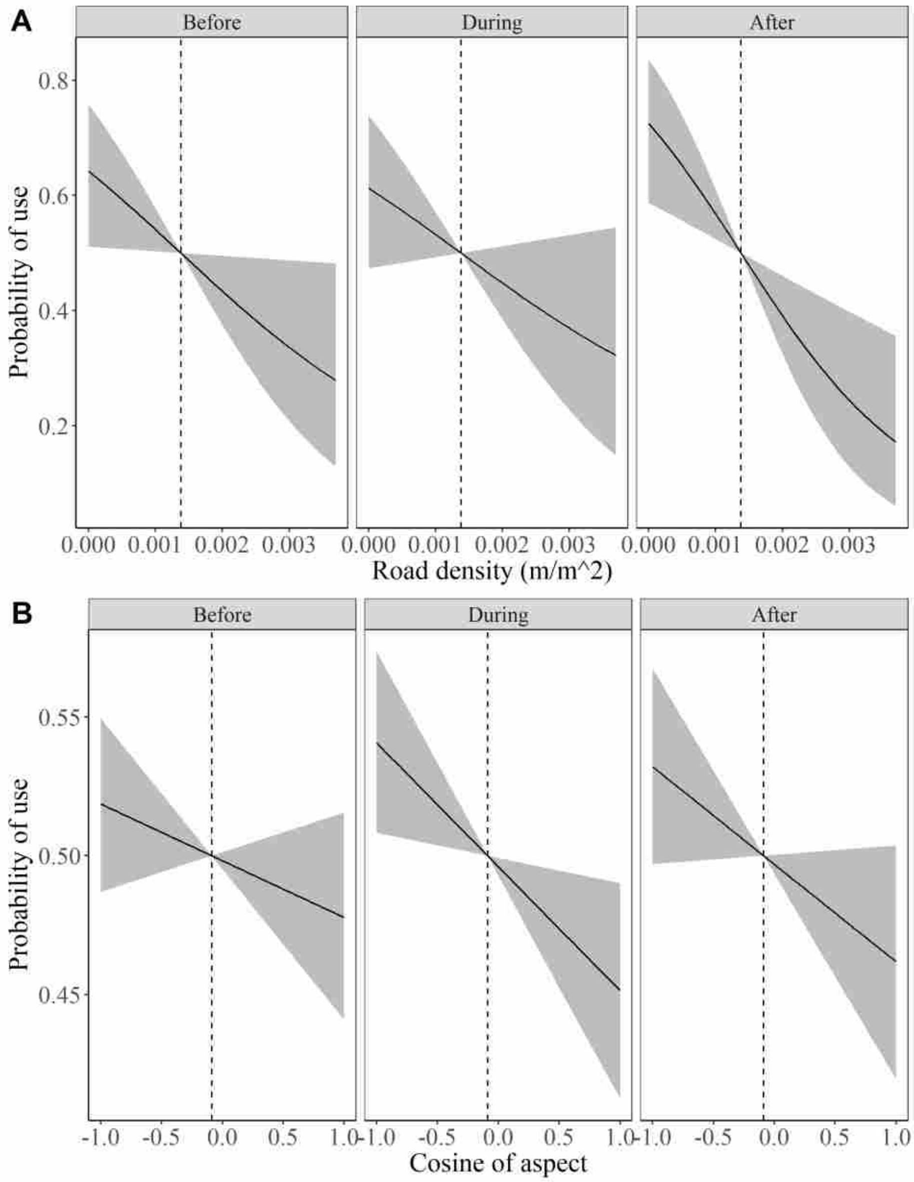

Figure 12. The probability of female white-tailed deer using a 30-m X 30-m cell before, during and after parturition as a function of A) Road density, and B) Cosine of the aspect (northerly aspect) in the Glaciated Plains region of Missouri, USA, 2015 – 2017. Each panel assumes a female deer is faced with 2 alternatives: the value of the covariate at the observed mean value (represented by the dashed vertical line) or an alternative value that varies along the x-axis. All other variables are assumed constant and fixed at their mean observed value. Black lines represent the mean posterior distribution and gray ribbons represent the 95% credible interval.

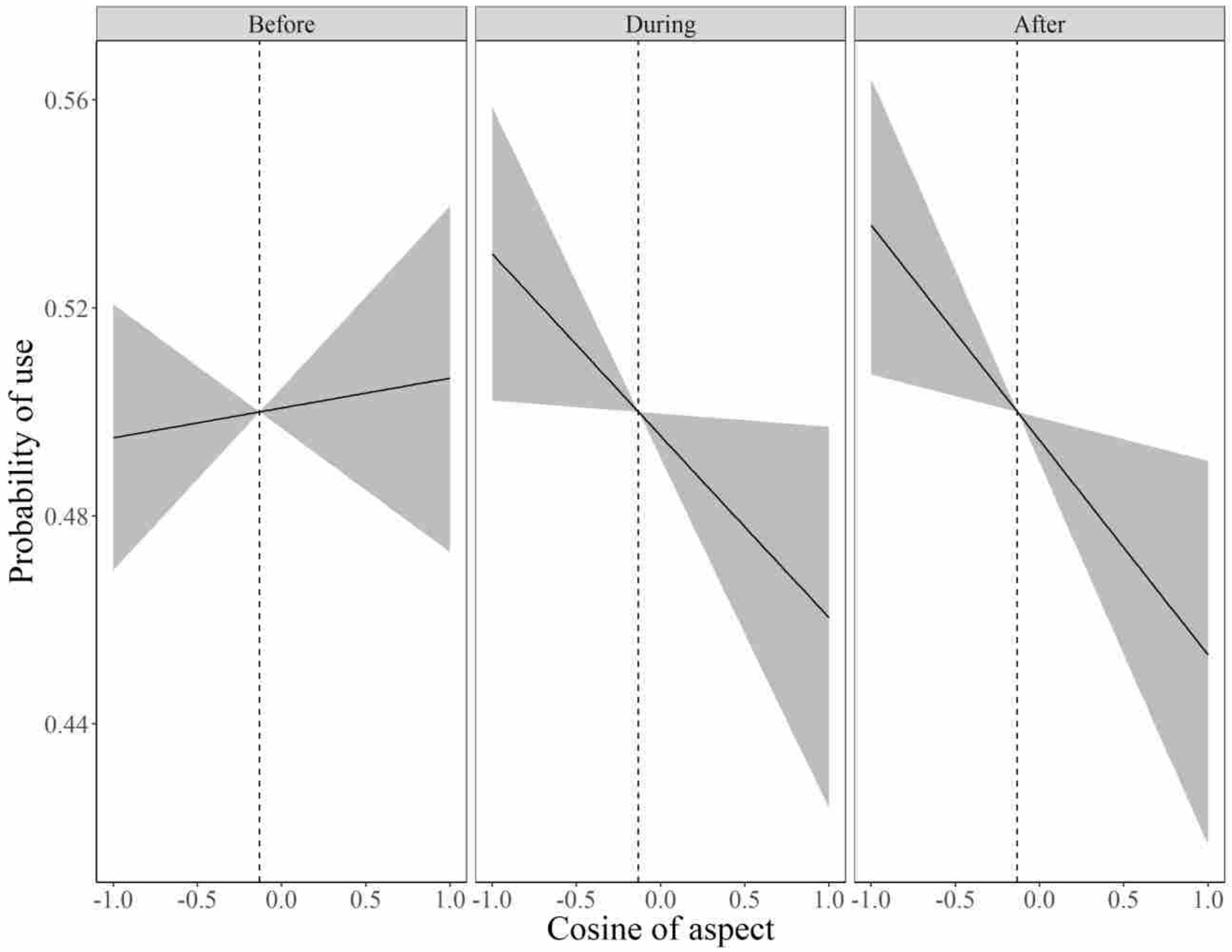

Figure 13. The probability of a female white-tailed deer in the Ozark region of Missouri, USA using a 30-m X 30-m cell as a function of the cosine of the aspect (northerly aspect) before, during, and after parturition. Each panel assumes the deer is faced with 2 choices: the mean northerly aspect, represented by the dashed vertical line, or an alternative value that varies along the x-axis. All other variables are assumed constant and fixed at their mean observed value. Black lines represent the mean posterior distribution and gray ribbons represent the 95% credible interval.

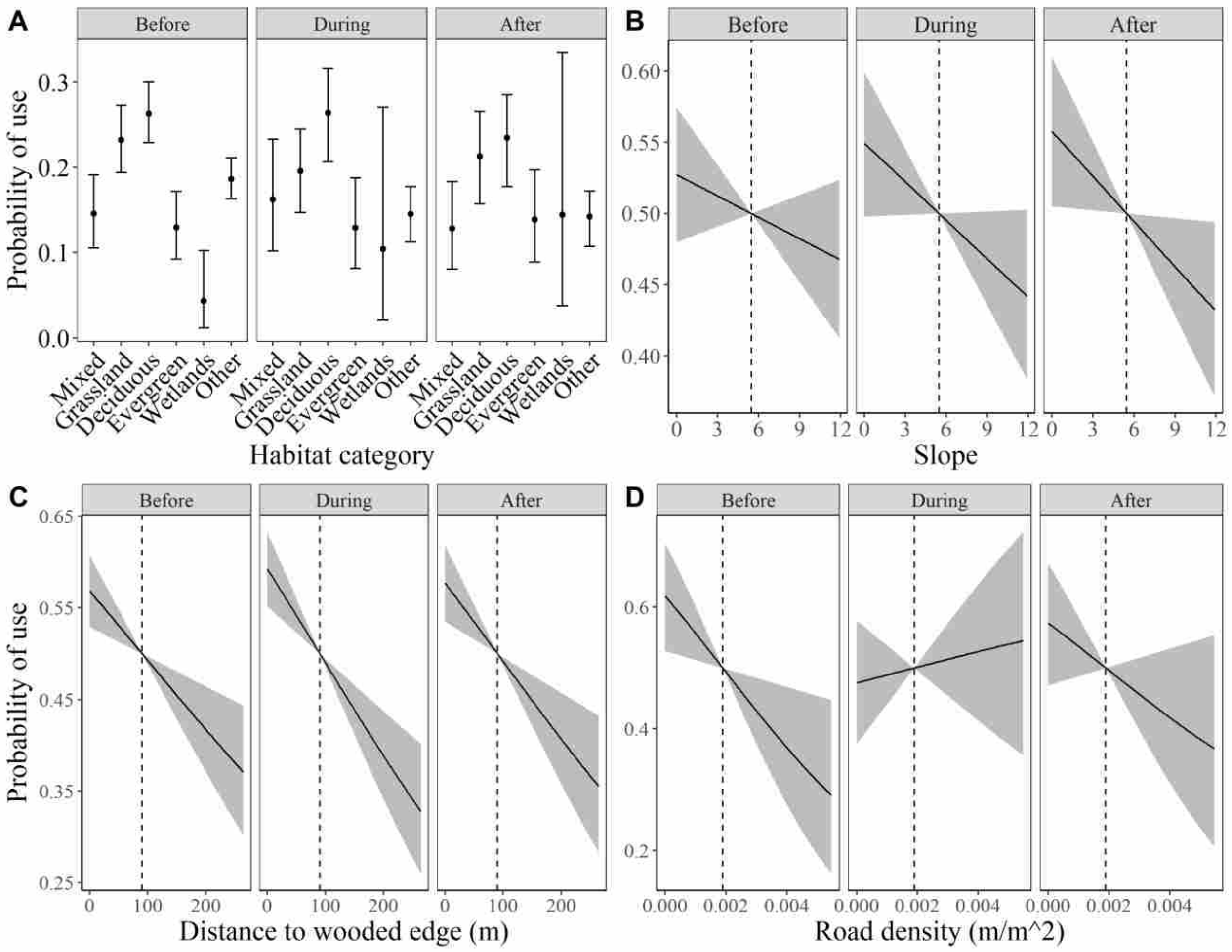

Figure 14. The probability of female white-tailed deer using a 30-m X 30-m cell before, during and after parturition as a function of A) Habitat category, B) Slope, C) Distance to nearest wooded edge, and D) Road density in the Ozark region of Missouri, USA, 2015 – 2017. Panel A assumes a deer is faced with 6 mututally exclusive alternatives to choose from. Circles represent the mean posterior distribution and error bars represent the 95% credible interval. Panels B – C assume a female deer is faced with 2 alternatives: the value of the covariate at the observed mean value (represented by the dashed vertical line) or an alternative value that varies along the x-axis. All other variables are assumed constant and fixed at their mean observed value. Black lines represent the mean posterior distribution and gray ribbons represent the 95% credible interval.

Chapter 3: Behavioral responses of female white-tailed deer (*Odocoileus virginianus*) to increased hunting pressure.

ABSTRACT

Predators can influence prey species indirectly by altering their behavior, which can have wide-ranging ecological effects. Throughout the mid-western United States recreational hunters have replaced natural predators as the leading cause of mortality for many white-tailed deer (*Odocoileus virginianus*) populations. Quantifying annual survival rates of female white-tailed deer, and understanding why and how deer respond to an increase in hunting pressure can help management agencies ensure their actions are having the desired effect on populations. We evaluated how differences in land use, habitat types, and habitat fragmentation affected white-tailed deer space use, movements, and resource selection before, during, and after the hunting season in the highly fragmented glaciated plains (GP) and more contiguous Ozark (OZ) eco-regions of Missouri. We also estimated annual survival rates of female deer in each of these regions. We created dam home ranges, calculated space use shifts, measured movement speed, and estimated resource selection for the 11 days before, during, and, after the rifle hunting season. We radio-collared a total 230 female deer from 2015-17, which we included in our annual survival estimates, and included 104 of those deer in our hunting season behavior analyses. Annual survival was similar between years in the GP at 0.816 (95% confidence interval [CI] = 0.754 – 0.884), but differed among years in the OZ (0.692 [95% CI 0.524 – 0.913] in 2015, 0.902 [95% CI = 0.830 – 0.979] in 2016, and 0.902 [95 % CI = 0.830 – 0.980] in 2017). Females in the GP increased their movement speeds by 7.86% during the hunting season, and were 13.2% greater after the hunting season compared to before. Similarly, in the OZ females increased their movement speeds by 5.07% during the hunting season and remained 8.23%

higher after the hunting season compared to before. Home range sizes were also larger during and after the hunting season in the GP, while in the OZ home range sizes were only elevated during the hunting season. Females in both study areas altered their use of resources during the study period, but most changes in selection occurred after the hunting season. We hypothesize that breeding movements overrode predator avoidance behaviors, which led to the similarity in movement behaviors during and after the hunting season in the two study areas. We further hypothesize that females shifted their resource use after the hunting season to increase their nutritional condition prior to winter. However, regardless of the mechanisms driving behavioral shifts during this time period we do not think that female deer made movements or selected for resources that would preclude them from being harvested.

KEY WORDS. White-tailed deer, hunting, movements, resource selection, survival, Missouri, predation, *Odocoileus virginianus,* breeding season

INTRODUCTION

In predator-prey systems predators can influence the demography and population dynamics of prey species directly through predation, and indirectly by modifying prey physiology (Creel et al. 2007), morphology (Kats and Dill 1998), and behavior (Preisser et al. 2005, Creel and Christianson 2008). Behavioral modifications made by prey to reduce their exposure to risk include increased vigilance levels (Altendorf et al. 2001), altered movement, foraging and activity patterns (Proffitt et al. 2009, Webb et al. 2011), and changes in group size (Gower et al. 2008) and habitat use (Creel et al. 2005). Often there are negative trade-offs associated with these changes in behavior such as foraging in sub-optimal habitats to avoid predators (Hernández and Laundré 2005), or increasing energy expenditure at times when gaining body mass is crucial (Ordiz et al. 2012, Paton et al. 2017). Selection is expected to favor individuals who optimally balance the costs and benefits of reducing risk. Prey behavioral responses can have wide ranging ecological effects including impacting prey population dynamics (Hik 1995), influencing food webs (Schmitz et al. 2000), and altering plant communities (Ripple et al. 2001, Estes et al. 2011).

In human dominated landscapes it has been suggested that humans elicit similar indirect, behavioral responses in prey species as natural predators (Frid and Dill 2002). For example, Shannon et al. (2014) found that anthropogenic road noise significantly reduced aboveground activity, reduced the time spent foraging, and increased vigilance of prairie dogs (*Cynomys ludovicianus*). Furthermore, Gude et al. (2006) found that the risk of being killed by hunters had a greater indirect effect on elk (*Cervus canadensis*) behavior than did the risk of being killed by wolves (*Canis lupus*). Recreational hunters have become the leading predators for many ungulate species throughout North America due to the extirpation of apex predators (Ripple et al. 2014). For example, hunter harvest is the leading source of mortality for adult elk in the United States (Keller et al. 2015), adult Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in Washington (Bender et al. 2004), and many populations of adult white-tailed deer (*Odocoileus virginianus;* Whitlaw et al. 1998, Brinkman et al. 2004, Anderson et al. 2015, Kilgo et al. 2016, Wiskirchen 2017).

In the absence of natural predators, management agencies use recreational hunting as a tool to help manage ungulate population sizes (Nixon et al. 1991, Hansen and Beringer 2003, Brinkman et al. 2004). Even with high harvest pressure, annual survival of adults can be high (Gaillard et al. 1998, Brinkman et al. 2004, DelGiudice et al. 2006), which can have negative impacts on the environment and society (Conover 2011, Côté 2011). Ungulates can change behavior patterns to minimize the risk of being predated upon (McLoughlin et al. 2005) or harvested, so it is important that we understand the spatio-temporal responses of ungulates to hunter predation risk. For example, Rhoads et al. (2013) found that white-tailed deer shifted their space use from areas where hunting was allowed to non-hunted refuge areas during a controlled hunt, thus reducing the efficacy of the hunt. Furthermore, Lone et al. (2015) found that red deer could reduce their susceptibility to being harvested by shifting their space use to more concealing cover habitat at the onset of the hunting season.

Previous research has evaluated the effect of hunting activity on ungulate behavior, but few consistent conclusions have been made. In some studies ungulates increased movement rates during the hunting season (Root et al. 1988, Naugle et al. 1997, Proffitt et al. 2006, Rhoads et al. 2013, Cleveland et al. 2012), while in others they decreased their movement rates (Autry 1967, Nixon et al. 1991, Little et al. 2014, Wiskirchen 2017). Other studies showed that ungulates exhibited site fidelity and shifted resource selection within their home ranges (Autry 1967, Root et al. 1988, Kilpatrick and Lima 1999, Marantz et al. 2016), while other studies indicated that ungulates shifted their space use away from their pre-hunt home ranges (VerCauteren and Hygnstrom 1998, Proffitt et al. 2006, Rhoads et al. 2013). Finally, Neumann et al. (2009) and Ericsson and Wallin (1996) found no significant change in moose (*Alces alces*) behavior as a result of increased hunting pressure. Possible explanations for this variability include differences between species, sexes (Lone et al. 2015), amount of hunting pressure (Autry 1967, Root et al. 1988, Neumann et al. 2009), habitat types (Proffitt et al. 2006), and the level of habitat fragmentation (Jayakody et al. 2008).

We used two contrasting study regions to determine how different habitat types and levels of fragmentation affected the behavioral response of female white-tailed deer (hereafter deer) to an increase in human predation risk. We calculated movement speed, space use, and habitat selection before, during, and after the hunting season to assess behavioral changes. We conducted this study in the Glaciated Plains (GP) and Ozark (OZ) regions of northwestern and south-central Missouri, which differ in land ownership, habitat, land use, and deer hunting regulations. We predicted that in the GP, where escape cover is minimal and highly fragmented, deer would increase their movement speed (Marshall and Whittington 1968, Root et al. 1988), shift their space use outside of their pre-hunt home ranges (Kammermeyer and Marchinton 1975, VerCauteren and Hygnstrom 1998, Rhoads et al. 2013), and select for hiding cover to minimize their predation risk (VerCauteren and Hygnstrom 1998, Kilpatrick and Lima 1999, Rhoads et al. 2013). In the OZ, where escape cover is abundant and contiguous, we predicted that deer would decrease their movement speed (Autry 1967, Nixon et al. 1991, Little et al. 2014), exercise site fidelity (Autry 1967, Root et al. 1988, Kilpatrick and Lima 1999, Marantz et al. 2016) and select for hiding cover within their home ranges.

In Missouri, deer are the only harvestable large mammal within state, and business revenue generated by harvesting deer exceeds $1 billion annually (Missouri Department of Conservation [MDC] 2013). Survival rates for deer in Missouri were last collected in the late 1980s and early 1990s when deer populations were growing rapidly. However, since this time there have been numerous changes to the deer population including a reduction in deer population size, declining growth rates, changes in harvest strategies, and the emergence and spread of chronic wasting disease (CWD), likely rendering these prior estimates outdated for use in population models and current management plans (MDC 2015). Thus, our second objective was to provide updated estimates of female survival to assist with ongoing white-tailed deer management in Missouri. Ensuring that deer continue to be managed at a level considered appropriate by the public is vital, so it is important that we understand deer survival rates and how and why deer respond to hunting pressure.

STUDY AREAS

Glaciated plains

The Glaciated Plains (GP) eco-region encompasses 32% of Missouri and is characterized by rich, productive soils. The GP study area included Andrew, Gentry, DeKalb, and Nodaway counties in northwest Missouri (Figure 1). The combined area of the 4 counties was 5779.29 km^2 and is 2.48% urban areas, 44.50% cultivated crops, 12.26% forest, 37.73% grassland, and 3.03% other. Land enrolled in the Conservation Reserve Program (CRP) made up 19.07% of the grassland vegetation (USDA Farm Service Agency [FSA] 2017). Publicly owned land made up 1.28% of the total area and was mostly comprised of conservation areas owned by the Missouri Department of Conservation (MDC). The most common land uses were farming of cultivated crops, with corn and soybeans totaling 36.98% and 50.86% of all crops grown, respectively, and raising cattle for beef and dairy production. The area was also characterized by low, rolling hills with elevation ranging from 185 m to 475 m, with local relief from 3 m to 30 m (United States Department of Agriculture [USDA] Natural Resources Conservation Service [NRCS] 2006).

The climate consisted of moderately cold winters and warm, humid summers. The mean annual temperature was 11.3^{o} C, with minimum temperatures in January (-8.86^{o} C) and highest temperatures in July (30.52^{o} C; Prism Climate Group, www.prism.oregonstate.edu, accessed 21 Jan. 2018). The average annual precipitation was 94.36 cm, with the lowest precipitation in January (2.1 cm) and the highest in June (13.04 cm; Prism Climate Group 2018).

Land not dominated by agriculture supported grassland vegetation and oak-hickory forest (NRCS USDA 2006). Common grass species included big bluestem (*Andropogon gerardi),* indiangrass (*Sorghastrum nutans*), little bluestem (*Schizachyrium scoparium),* switchgrass *(Panicum virgatum),* and wildrye *(Elymus* spp.*).* Upland wooded areas supported southern red oak *(Quercus falcata*), white oak *(Q. alba*), hackberry *(Celtis* spp.*),* shagbark hickory *(Carya ovata*) and bitternut hickory *(C. cordiformis).* Bottomland wooded areas included sycamore *(Platanus occidentalis),* cottonwood *(Populus* spp.), elms *(Ulmus* spp.), green ash *(Fraxinus pennsylvanica*) and silver maple *(Acer saccharinum).* At the time of this study deer density in the 4 county area was approximately 7 deer/km^2 (K. Wiskirchen, Missouri Department of Conservation, personal communication). Coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) were the two most common predators, with 5 confirmed mountain lion (*Puma concolor*) sightings in the GP since 2006.

Ozarks

The Ozark (OZ) eco-region encompassed 38% of Missouri and was characterized by thin, rocky soils. The OZ study area included Douglas, Howell, Texas, and Wright counties in south-central Missouri (Figure 1). The combined area of the 4 counties was 9,332.25 km^2 and was 2.09% urban areas, 1.69% cultivated crops, 52.65% forest, 42.98% grassland, and 0.59% other. Publicly owned land comprised 14% of the Ozark region and the 4 county area included 600 km^2 of Mark Twain National Forest. The most common land use was the raising of cattle for beef and dairy production, with a total of 3,766 farms with 279,868 head of cattle throughout the four counties (USDA National Agricultural Statistics Service [NASS] 2012). The topography was highly variable, with elevation ranging from 90 m to 500 m and local relief anywhere from 60 m to 240 m (Thom and Wilson 1980, NRCS USDA 2006). Caves, springs, bluffs and clear-flowing streams were characteristic features of the area.

The climate consisted of moderately cold winters and warm, humid summers. The mean annual temperature was 13.26° C, with minimum temperatures in January (-5.39° C) and high temperatures in August (31.5° C; Prism Climate Group 2018). The average annual precipitation was 115.11 cm, with the lowest precipitation in January (6.63 cm) and the highest in May (12.72 cm; Prism Climate Group 2018).

The OZ was mostly oak-hickory and oak-hickory-pine forests (NRCS USDA 2006). The dominant tree species were black oak (*Quercus velutina*), scarlet oak (*Q. coccinea*), white oak (*Q. alba*), post oak (*Q. stellata*), hickory (*Carya* spp.), and shortleaf pine (*Pinus echinata*). Most non-forested areas were created for pasture or hay fields, but some natural glades occurred and supported warm-season grasses, such as big bluestem, indiangrass, and little bluestem. At the time of this study, deer density in the 4 county area was approximately 9 deer/km^2 (K. Wiskirchen, personal communication). Coyotes and bobcats were the predominant predators in the area, although a small, recolonizing black bear (*Ursus americanus*) population existed in the southern OZ region. There have been < 45 confirmed mountain lion sightings in the entire OZ region since 2006.

METHODS

White-tailed Deer Capture and Mortality Investigations

We captured fawn (6-9 month old), yearling (1.5 year old) and adult (>1.5 years old) female deer using modified Clover traps (VerCauteren et al. 1999) and rocket nets (Haulton et al. 2001) from January – March 2015 – 2017. All captured deer received a uniquely numbered metal ear tag (Hasco Tag Company, Dayton, KY). Yearling and adults were fitted with a 825 g Iridium GPS radio-collar (Model G2110E, Advanced Telemetry Systems) and fawns in 2016 were fitted with a 550 g Iridium Lite GPS radio-collar (Model G2110L, ATS) that were programmed to record a location every 5 hours. However, we programmed collars to record a location once every 90 mins from 31 October – 10 December in 2015 and 2016, to better capture fine scale changes in movements and space use surrounding the hunting season.

Collars were equipped with an 8-hour motion sensitive switch that alerted us remotely when the collar remained motionless. We also caught and VHF collared neonates from mid-May through mid-June each year (see Chapter 1 for details), that we included in our survival analysis as a part of the fawn age class if they survived until they were recruited to the population. All collars were labeled with a phone number for hunters to call and report harvesting a collared deer. All capture and handling procedures were approved by the Institutional Animal Care and Use Committee at the University of Missouri (protocol number 8216).

When we detected a mortality signal we located the radio-collar as fast as possible, but given constraints with land access we were not always able to investigate the mortality that same day. Therefore, it was likely that scavenging occurred before we reached the carcass, so we were conservative when assigning cause of death. Predation of adult deer is uncommon in areas of the Midwest with similar predator species (Nixon et al. 1991, Hansen and Beringer 2003, Brinkman et al. 2004), so we did not assign predation as cause of death unless we had conclusive evidence, such as killing bite marks in the head or neck (White 1973).

Study Design

To determine if female white-tailed deer altered their behavior in response to increased hunting activity we selected the time period in which hunting pressure was the greatest (Autry 1967, Root et al. 1988), the November portion of the firearms season (hereafter firearms season). During this 11 day period between 60-70% of the total harvest occurs (MDC 2018), and hunter densities are approximately 1.57 and 1.68 hunters/km^2 in the OZ and GP, respectively (K.

Wiskirchen, personal communication). Ideally we would compare behavior during the firearms season to a similar time of year when no harvest occurs (Little et al. 2014, 2016). Unfortunately, a comparison between behavior in hunting and non-hunting periods is not feasible in Missouri because archery hunting exists continuously from mid-September through mid-January, with youth, antlerless rifle, and alternative methods seasons also falling within that time frame. However the hunting seasons that directly precede and follow the firearms season have much lower hunter densities and harvest rates (17 – 20% of total harvest in archery, 3 – 4% antlerless firearms; MDC 2018). Therefore it is likely that deer are less affected by the low hunting pressure surrounding the firearms season, so we compared behavior during the 11 day firearms season to the 11 days directly before and after the firearms season in 2015 and 2016.

The November portion of the firearms hunting season ran from 14 November – 24 November 2015 and 12 November – 22 November 2016. Legal shooting hours began half an hour before sunrise and ended half an hour after sunset. The 'before' hunting period refers to 3 November – 13 November 2015 and 1 November 2016 – 11 November 2016. The 'after' hunting period refers to 25 November 2015 – 5 December 2015 and 23 November 2016 – 3 December 2016.

Survival Analysis

We estimated annual female survival rates using the Andersen-Gill (AG) formulation of the Cox proportional hazards model (CPH) with a recurrent time scale, using 1 April as the start date each year (Andersen and Gill 1982, Fieberg and DelGiudice 2009). The CPH model is well suited to handle the range and variability of hazards found in wildlife populations because it does not assume a specific hazard function (Murray 2006). The assumptions of the AG model are that censoring is independent of survival, individual fates are mutually independent, covariates vary linearly with the log hazard and that hazard ratios between individuals are proportional and remain constant over time. We tested the proportional hazards assumption by plotting the scaled Schoenfeld residuals for each variable against time (Grambsch and Therneau 1994, Johnson 2004), using the package survival (Therneau 2017) in Program R version 3.4.3 (R Core Team 2017). We tested all models, but only report results if we saw a significant violation of the assumption.

We created 5 different models to explain female survival, and included year (2015, 2016, 2017) and age class of the deer (fawn, yearling, adult) as covariates. We aged all deer up one age class on the 1 June each year, which was close to the average date of birth in both study areas (Hansen et al. 1996, Chapter 1). We included fawns collared as neonates in our survival analysis if they survived until 15 September of the year they were collared. We chose 15 September because that was the onset of the archery hunting season and we considered neonates to be recruited to the population at that time (Rohm et al. 2006).We excluded mortalities that occurred < 30 days post capture in our survival analysis because we were unable to rule out capture myopathy as a cause of death (Beringer et al. 1996). We right censored deer when collars were either removed as designed or when they stopped working. We used Akaike's information criterion adjusted for small sample sizes (AIC_c) to determine the best model in the candidate set and considered models within 2 ΔAIC_c units as competing for the top model (Burnham and Anderson 2002). If models within this threshold only differed from the top model by one additional parameter we considered that parameter to be uninformative and unsupported by the data. We ran all survival models using individual deer identification as a cluster variable within the package survival (Fieberg and DelGiudice 2009, Therneau 2017) and conducted model selection using the package AICcmodavg (Mazerolle 2016) in Program R.

Movement Characteristics

We evaluated the influence of age (yearling or adult), land ownership (public or private), forested cover, time of day (crepuscular, day, night), and the period of the hunting season (before, during, after) on female deer movement speed. We excluded all collar locations where the GPS positional dilution of precision (PDOP) reading was > 10 (D'Eon and Delparte 2005) and locations that were taken > 24 hours apart. We calculated the time and distance between successive locations using the geosphere package (Hijmans et al. 2017*a*) in Program R, and computed the movement speed in meters per hour. We used the maptools package (Bivand et al. 2017) in program R to determine sunrise, sunset, start of nautical dawn, and nautical dusk at each specific location. We obtained a layer of public lands in all 8 study area counties from the U.S. Department of Agriculture-Geospatial Data Gateway (USDA-GDG) and created a raster layer using the raster package (Hijmans et al. 2017*b*) in Program R that classified each 30-m X 30-m pixel as public or private land. We obtained the 2011 land use land cover (LULC) layer from the National Land Cover Database (NLCD; Homer et al. 2015) for all 8 study area counties, and used the raster package (Hijmans et al. 2017*b*) in Program R to re-classify each pixel as either forested (included deciduous, evergreen, mixed forests) or non-forested. We assigned each location as forested or non-forested, public or private, and the time of day the location was taken: day, night, or crepuscular. Day time locations occurred from 1 hour after sunrise to 1 hour before sunset, night occurred from nautical dusk to nautical dawn, and crepuscular was nautical dawn to 1 hour after sunrise and 1 hour before sunset to nautical dusk. We aged all deer in the same manner as described above.

We predicted that increased forest cover would act as increased escape cover and thus reduce movement speeds during the hunting season (Pilcher and Warmpler 1981, VerCauteren and Hygnstrom 1998), and that hunting pressure would be higher on public land than private land (Root et al. 1988), thus affecting deer movement speeds during the hunting season. We predicted that time of day would have the greatest influence on deer movement speed (Beier and McCullough 1990), but that deer would alter their movement speeds differently during daylight hours (legal shooting hours) compared to nocturnal hours (Kilgo et al. 1998, Little et al. 2015, Wiskirchen 2017). However, we predicted that the direction of these changes would be dependent of the study area, with decreased diurnal movement speeds but increased nocturnal speeds during the hunting season in the OZ, and the opposite in the GP. To test these hypotheses we used the information theoretic approach (Burnham and Anderson 2002) and developed a set of candidate models for each study area (Table 1). Deer in the GP used almost exclusively private land, so we did not include land ownership as a covariate in the GP models. We log transformed movement speed and ran each model as a linear mixed model with deer identification as a random effect using the lme4 package (Bates et al. 2017) in Program R. We selected the best approximating model using AIC_c (Burnham and Anderson 2002) using the AICcmodavg package (Mazerolle 2017) in Program R as described above.

Space Use

To evaluate the influence of forest cover, age, land ownership, and period of hunting on female deer space use we calculated home ranges in each period using the dynamic Brownian bridge movement model (dBBMM; Kranstauber et al. 2012) using the move package (Kranstauber et al. 2017) in Program R. The dBBMM computes home ranges by creating a utilization distribution (UD; Worton 1989) that incorporates both the size of the area of use and the animal’s intensity of use within this area. The dBBMM creates a UD by modeling the space use between 2 continuous locations as Brownian movement, a continuous random walk in which movement is diffusive and equally likely in any direction (Turchin 1998, Horne et al. 2007). The dBBMM requires the fixed position, time of each location, error associated with the locations (GPS collar error), and the degree to which movement between locations deviates from a straight line, also known as the magnitude of variance of the Brownian motion (σ_m^2). To account for behaviorally distinct movements that change over time, the dBBMM allows σ_m^2 to vary along the movement path (Gurarie et al. 2009, Kranstauber et al. 2012) using an adjusted version of the behavioral change point analysis (Gurarie et al. 2009) via a sliding window with *w* locations along a path. The window moves along the movement path and calculates a new σ_m^2 for each step every time it falls within the window. These σ_m^2 estimates are averaged to get a final σ_m^2estimate for each step.

Choosing the size of the window is a critical step because a tradeoff exists between the greater reliability in the estimation of σ_m^2 with a large window size and the short term changes that can be detected with a small window. Also, a margin (*m*) greater than 3 locations is needed on either end of the window in which no break points can occur. We used a window size of 7 (equivalent to 10.5 hours), and a margin of 3 that we chose based on the cross-validation techniques suggested by Kranstauber et al. (2012). We used a GPS collar error of 5.92 m that we determined by performing GPS collar accuracy field tests (Appendix A).

We used 95% volume contours to define the home range area (ha), and only estimated the home range area for deer during a period provided they had at least 50 total locations and 7 days' worth of locations in that period. We used the same land ownership and forest layers developed for the movement speed analysis, and used the SDMTools package (VanDerWal et al. 2014) in Program R to compute the proportion of each home range that was forested (0 – no forest, 1 –

completely forested) and private land (0 – all public, 1– all private). We aged deer in the same manner as before, and assigned each home range to its respective period of hunting.

We predicted that increased forest cover would act as increased escape cover and thus reduce home range sizes during the hunting season (Pilcher and Warmpler 1981, VerCauteren and Hygnstrom 1998), and that hunting pressure would be higher on public land than private land (Root et al. 1988), thus also affecting home range size during the hunting season. We also predicted that home range sizes would be smaller in the OZ during the hunting season, but larger in the GP compared to before and after the hunting season. To test these hypotheses we used the information theoretic approach (Burnham and Anderson 2002) and developed a set of 19 candidate models in each study area (Table 2). Deer in the GP used almost exclusively private land, so we did not include land ownership as a covariate in the GP models. We log transformed home range size and ran each model as a linear mixed model with deer identification as a random effect using the lme4 package (Bates et al. 2017) in Program R. We selected the best approximating model using AIC_c (Burnham and Anderson 2002) using the AICcmodavg package (Mazerolle 2017) in Program R as described above.

We used the volume of intersection index (VI; Millspaugh et al. 2000, 2004) to evaluate whether deer spatially shifted their core area of use (50% volume contour; Kilpatrick et al. 2001) as a result of increased hunting pressure. The VI measures the degree of overlap between 2 or more UDs by determining the volume between the 3-dimensional surface and the x and y planes of each UD (Millspaugh et al. 2000). The VI value ranges between 0 and 1, and we can interpret the VI value as the percentage of overlap in the UDs between the two time periods, with a score of 0 indicating no overlap (space use completely different between the 2 time periods) and a score of 1 indicating complete overlap (space use the same between 2 time periods; Millspaugh et al. 2000).

We computed up to 3 VI scores for every deer using the adehabitatHR package (Calenge 2006) in Program R. The VI scores were calculated by comparing space use before and after the hunting periods, before and during the hunting period, and during the hunting period to after. We created 5 different models that we thought would best explain the variation in VI scores, and included age of the deer during the hunting season and the comparison made as covariates. We log transformed the VI scores and ran each model as a linear mixed model with deer identification as the random effect using the lme4 package (Bates et al. 2017) in Program R. We selected the best approximating model using AIC_c (Burnham and Anderson 2002) in the AICcmodavg package (Mazerolle 2017), as described above.

Resource Selection

We determined third order resource selection (within home range; Johnson 1980) for female deer before, during, and after the firearms season by comparing resource attributes at points where deer were located (used locations) to attributes at random points that were considered available (available locations). Defining resource availability is a critical component of a resource selection study (Buskirk and Millspaugh 2006). We uniquely defined availability at each used point to ensure that all the resources classified as available were available to the animal at that time; this is known as creating a choice set (Cooper and Millspaugh 1999). We determined availability by selecting 5 random points within a circle created using the radius of available habitat method (Durner et al. 2009). This method creates a circle centered on the deer’s previous location using the equation

$$radius\ of\ avilable\ habitat = c(a + 2b)$$

where *a* is the mean hourly movement rate, *b* is the standard deviation of the movement rate and *c* is the number of hours between locations (Durner et al. 2009). We calculated the mean hourly movement rate for the 3 different hunting periods in each study area to account for differential movement rates during these times (Rhoads et al. 2013). If the used location occurred outside of the circle created using this method, we defined the radius as the straight line distance between the previous and used location (Durner et al. 2009). We used the geosphere package (Hijmans et al. 2017*a*) in Program R to calculate the movement rates and hours between locations.

We defined 10 resource attributes within 30-m X 30-m cells which we called resource units (Table 3). We used the LULC layer downloaded previously and reclassified the land cover types into the 7 most commonly found throughout our study areas (Table 4). We calculated contagion, which measures the degree to which patch types of the same land cover type are clumped together using FRAGSTATS version 4.2 (McGarigal et al. 2012). We calculated contagion within a circle defined by the average radius of available habitat for all deer (620 m; Durner et al. 2009). To determine if deer selected for areas closer to cover (in this case forest) we calculated the distance to the nearest wooded edge. To improve model fit, in the OZ we log-transformed distance to wooded edge to include the pseudo-threshold functional form (Franklin et al. 2000). We used the geospatial modeling environment (GME; Beyer 2012) to extract the edges between forests and open areas (grassland, cropland) from the LULC layer and then used the rgeos package (Bivand et al. 2017) in Program R to determine the distance to edge. We also calculated the largest forest patch within 620 m of each used and available location using the SDMTools (VanDerWal et al. 2014) package in Program R.

We obtained the 2011 percent canopy cover layer from the USFS NLCD and 10 m demographic elevation models (DEM) for all 8 study area counties from the USDA-GDG. We used Surface Tools in ArcGIS 10.3 (Environment Research System Institute Inc., Redlands, CA) to calculate aspect class (north, east) and slope (degrees) from the DEM's. We calculated road density and distance to road to account for potential human disturbance. We calculated road density as meters of roads per square meter contained within a circle with a radius equal to the mean radius of available habitat to deer in each study area using the rgeos package (Bivand et al. 2017*a*) in Program R. We acquired our road layers using TIGER 2016 road data acquired from the US Census Bureau.

We used a case control model with contaminated controls (Rota et al. 2013) to fit our resource selection models. This model reliably estimates the parameters of a resource selection probability function (RSPF) using use-availability data and therefore provides an estimate of the absolute probability of use of a resource (Lele 2009, Rota et al. 2013). Estimating a RSPF is preferred over a resource selection function (RSF) because a RSF is proportional to the RSPF up to an arbitrary constant and only provides the relative probability of use of a resource, which can be meaningless when baseline probabilities are close to 0 or 1 (Keating and Cherry 2004). Absolute probabilities are also more intuitive to interpret than relative probabilities and can be used in straightforward comparisons of resource selection between studies and species (Rota et al. 2013).

A logistic regression analysis for resource selection estimates the probability that a species uses discrete sample units, and determines the effects that a variety of *m* covariates, written as $x_1, \ldots, x_m$, may have on the probability of using each sample unit. The probability that a species uses sample unit *i* can be written as:

$$\psi_i = \frac{e^{\beta_0 + \beta_1 x_{i1} + \ldots + \beta_m x_{im}}}{1 + e^{\beta_0 + \beta_1 x_{i1} + \ldots + \beta_m x_{im}}} \quad (1)$$

where ψ_i is the probability that a species occurs in sample unit i, β_0 is the intercept parameter, and $\beta_1, \ldots, \beta_m$ are the parameter coefficients associated with the m covariates (Millspaugh et al. 2018). Logistic regression assumes that use and non-use of sample units are known. However with use-availability data, the type of data used in this study, it is not known if available sample units are unused or if use was just not observed (Millspaugh et al. 2018). The case control model with contaminated controls deals with this issue by collecting a random sample of used sample units n_1 from the population of all used sample units N_1 and a sample of available sample units n_a, without regard to use or non-use, from the entire population of sample units N (Rota et al. 2013, Millspaugh et al. 2018). The probability that a sample unit is observed to be used, conditional on that sample unit being included in the sample is

$$\phi_i = \frac{\frac{h}{\pi(1-h)}\psi_i}{1+\frac{h}{\pi(1-h)}\psi_i} \quad (2)$$

where $h = n_1 / n$, and $n = n_a + n_1$, ψ_i is the probability of use defined in eqn. 1, and π is the unconditional probability of use of a sample unit, called prevalence (Lancaster and Imbens 1996, Keating and Cherry 2004, Rota et al. 2013, Millspaugh et al. 2018). We estimated prevalence independently within each of our study areas to be 0.64 in the GP and 0.84 in the OZ (Appendix B). The log-likelihood of the use availability model can then be written as

$$\ln\big(L(\beta_0, \beta_1, \ldots, \beta_m)\big) = \sum_{i=1}^{n} z_i \ln(\phi_i) + (1 - z_i)\ln(1 - \phi_i) \quad (3)$$

where $z_i = 1$ if sample unit i was observed to be used, 0 otherwise (Millspaugh et al. 2018).

We modeled the probability that a deer used a sample unit as a function of the resource attributes in Table 3 with unique deer ID included as a random effect. We also included interactive effects between the resource attributes and the period of hunting, both as defined above. We used a Bayesian implementation of the model and fit the model in JAGS (Plummer 2003) via the package R2Jags (Su and Yajima 2015). We assumed independent *normal*(μ=0, σ^2= 1000) prior distributions for the regression coefficients and assumed independent *normal*(μ=0.64, σ^2=0.20) prior distribution for π in the GP and *normal*(μ=0.84, σ^2=0.20) prior distribution for π in the OZ (Rota et al. 2013). We simulated 3 posterior chains for each study area, running each chain until adequate convergence was achieved ($\hat{R} < 1.1$; Gelman et al. 2014). We thus ran the 3 chains in the GP for 100,000 iterations each, discarding the first 4,000 as burn-in and keeping every second iteration thereafter, resulting in 144,000 saved iterations. In the OZ we ran the 3 chains for 106,000 iterations each, discarding the first 6,000 as burn-in and keeping every second iteration thereafter, resulting in 150,000 saved iterations.

We evaluated goodness of fit of the model with posterior predictive checks (Kéry and Schaub 2012, Gelman et al. 2014). We calculated the deviance function (McCullagh and Nelder 1989) from observed data (T_y) and from data simulated assuming the model was the data-generating model (T_{rep}). We then calculated a Bayesian *p*-value $p_B = \Pr(T_{rep} > T_y)$ from posterior simulations and assumed reasonable fit if $0.1 < p_B < 0.9$. We did not conduct model selection to determine a top model but rather based inference on habitat selection from the posterior distribution of the population-level parameter and its 95% credible interval using a global model. Specifically, we interpreted predictors with 95% credible intervals that did not overlap 0 as important variables in the habitat selection model (Beatty et al. 2014).

RESULTS

During 2015 – 2017 we caught and marked 183 female fawn, yearling, and adult deer with GPS collars (Table 5). Additionally, 47 VHF collared neonates survived until 15 September of the year they were collared and became a part of the fawn age class used in the survival analysis

(Table 5). In our hunting season analyses we only used data from 2015 – 2016 and included 104 different yearling and adult female deer (Table 5). We observed 47 mortalities (26 GP, 21 OZ) between 1 April 2015 and 31 Dec 2017. In the GP we attributed 9 mortalities to hunter harvest, 3 to wounding loss during the hunting season, 4 to vehicle collisions, 1 to epizootic hemorrhagic disease (EHD), 3 to suspected EHD, and 6 unknown. In the OZ we attributed 5 mortalities to hunter harvest, 3 to wounding loss during the hunting season, 2 to vehicle collisions, 1 to suspected EHD, and 10 unknown.

Survival

Glaciated Plains – We considered the null model ($\Delta AIC_c = 0.48$, $\omega_i = 0.32$) to be the most supported survival model, indicating that survival was similar between years and age classes. The top ranked model included year ($\Delta AIC_c = 0.00$, $\omega_i = 0.40$) but not all years were significant, so we considered it to be an uninformative model. Annual survival was 0.816 (95% confidence interval [CI] = 0.754 – 0.884; Figure 2a) in the GP.

Ozarks – We considered the top ranked survival model to be the top model, which included year ($\omega_i = 0.64$). Survival was lower in 2015 compared to 2016 ($\beta = -1.27$, 95% CI = -2.30 – -0.24) and 2017 ($\beta = -1.27$, 95% CI = -2.36 – -0.18). Survival was 0.692 (95% CI = 0.524 – 0.913) in 2015, 0.902 (95% CI = 0.830 – 0.979) in 2016, and 0.902 (95% CI = 0.830 – 0.980) in 2017 (Figure 2b, c, d). In both study areas, the risk of mortality was highest during the fall (15 September – 15 December), and lowest in the spring (16 March – 15 May; Figure 2).

Movement and space use metrics

Glaciated Plains – We considered time of day × forest + period ($\omega_i = 0.99$) as the top supported model for movement speed. The rest of the models were ≥ 10.39 ΔAIC_c away from the top model. Deer increased their movement speed by 7.86% and 13.20% during ($\beta = 0.88$, 95%

CI = 0.85 – 0.92) and after the hunting season (β = 0.95, 95% CI = 0.91 – 0.99), respectively, compared to before the hunting season (Figure 3). Deer also varied their movement speed depending on the time of day, with the fastest movements made during crepuscular hours (β = 3.93, 95% CI = 3.66 – 4.21), followed by night (β = 1.96, 95% CI = 1.85 – 2.07) and the slowest movements during the day. Deer moved faster in non-forested areas compared to forested areas (β = 1.02, 95% CI = 0.96 – 1.09), but the magnitude of this effect was greatest during crepuscular (β = 0.79, 95% CI = 0.72 – 0.88) and night time hours (β = 0.73, 95% CI = 0.67 – 0.79; Figure 3).

We identified 2 plausible models as the best explanations of home range size, forest × age + period (AIC_c = 252.52, ω_i = 0.57), and forest + period (AIC_c = 254.76, ΔAIC_c = 2.24, ω_i = 0.19). The weight of evidence supporting these 2 models combined was >10 times the weight supporting the next best model so we did not consider any other models to be supported by the data. The two models differed by the inclusion of the interaction term forest × age (β = 0.19, 95% CI = 0.05 – 0.67) and age (β = 1.75, 95% CI = 1.09 – 2.80), which we considered to be important parameters. Therefore we considered the top ranked model to be the best approximating model and used those β estimates to draw conclusions. Doe home range size was the smallest before the hunting season and increased by 23.48% during (β = 1.23, 95% CI = 1.07 – 1.42) and 15.76% after the hunting season (β = 1.15, 95% CI = 1.01 – 1.34; Figure 4). Doe home range size decreased as the proportion of forest within the home range increased (β = 0.11, 95% CI = 0.04 – 0.26), but the magnitude of this effect was dependent on the age of the doe (Figure 4).

In the GP all models used to explain the variation in core area overlap before, during and after the hunting season were within 4.24 ΔAIC_c from each other (Table 6). The top model included period of hunting (During: β= 1.06, 95% CI = 1.01 – 1.10; After: β= 1.06, 95% CI = 1.01 – 1.10), and the second best model differed only by the addition of the age parameter, which we determined was uninformative. The top model was only 3.56 ΔAIC_c from the null model, so the effect of hunting period on VI scores should be interpreted with caution. According to the top model females had the most similar space use during and after the hunting season, and had the least similar space use before and after the hunting season (Figure 5a). However, the space use overlap of core areas was low (27% – 37%) for all 3 comparisons (Figure 5a).

Ozarks – We considered time of day × forest + period (ω_i = 1) as the model that best explained movement speed during the hunting season. The rest of the models were ≥ 17.70 ΔAIC_c away from the top model. Deer responded to increased hunting pressure by increasing their movement speed by 5.07% during (β = 0.97, 95% CI = 0.94 – 1.00), and 8.23% after the hunting season compared to before (β = 0.92, 95% CI = 0.89 – 0.96). Deer also varied their movement speed depending on the time of day, with slowest movements made during the day (β = 0.57, 95% CI = 0.53 – 0.60), and fastest movements made during crepuscular hours (β = 1.69, 95% CI = 1.58 – 1.81). Deer moved faster in non-forested areas compared to forested areas (β = 1.02, 95% CI = 0.96 – 1.09), but the magnitude of this effect depended on the time of day (Day: β = 1.42, 95% CI = 1.22 – 1.42, Crepuscular: β = 1.4, 95% CI = 1.05 – 1.23; Figure 6).

We considered age × forest + period (AIC_c = 344.07, ω_i = 0.84) to be the model that best explained doe home range size. The second ranked model was 5.49 ΔAIC_c from the top model and the weight of evidence supporting the top model was ≥ 16 times the second ranked model. Female home range size was different for yearlings and adults (β = 0.32, 95% CI = 0.15 – 0.69), and home range size increased as the proportion of forested cover within the home range increased (β = 1.03, 95% CI = 0.58 – 1.82), but this effect was mainly observed in yearlings (β =

9.85, 95% CI = 2.94 – 33.04; Figure 7). Furthermore, females increased the size of their home range by 25.11% during the hunting season (β = 1.25, 95% CI = 1.04 – 1.51), and reduced it back to pre-hunt size after the hunting season (β = 0.97, 95% CI = 0.84 – 1.12).

In the OZ the model that best explained variation in space use overlap only included period of hunting as a parameter (During: β= 1.09, 95% CI = 0.92 – 1.10; After: β= 1.13, 95% CI = 1.08 – 1.18; Table 6). The second and third most supported models had more parameters but essentially the same maximized log-likelihood so we removed those models from consideration. According to the top model females had the most similar space use during and after the hunting season, and had the least similar space use before and after the hunting season (Figure 6b). However, the space use overlap of core areas was low (21% – 36%) for all 3 comparisons (Figure 6b).

Resource selection

Glaciated Plains – We modeled female resource selection based on 29,062 used locations and 144,345 available locations. The average radius of available habitat was 684.12 m. We achieved convergence for all hyper-parameters in the model ($\hat{R} \leq 1.1$) and adequate goodness of fit for this model (Bayesian p-value = 0.40). The model estimated the probability of a female using any 30-m X 30-m grid cell on the landscape (prevalence) to be 0.53 (95% credible interval 0.51 – 0.54).

Female white-tailed deer altered their use of some resources before, during, and after the hunting season (Table 7). Before and during the hunting season females were less likely to use 30-m X 30-m cells on the landscape that were south facing, but more likely to use cells closer to wooded edges, compared to after the hunting season (Table 7, Figure 8a and b). Before and after the hunting season females were more likely to use areas with lower contagion values, while during the hunting season females showed no preference for contagion values (Table 7, Figure 8c). Females were also slightly more likely to use areas with lower percent canopy cover during and after the hunting season, as compared to before (Table 7, Figure 8d). Females were consistently more likely to use steeper slopes and areas farther from roads during all 3 periods of the hunting season (Table 7, Figure 9a and b).

During all 3 periods of the hunting season females were more likely to use forested areas than any other type of habitat on the landscape (Table 7, Figure 10). Grassland areas were the next most likely to be used landscape category, and their use increased after the hunting season (Table 7, Figure 10). Females were less likely to use wetland habitats during the hunting season than before the hunting season, and this habitat type was also consistently the least likely landscape category to be used during any period of the hunting season (Table 7, Figure 10). Females were also more likely to use crop fields after the hunting season compared to before (Table 7, Figure 10). Females showed no selection for or against habitat types in the other category.

Ozarks – We modeled female resource selection based on 37,104 used locations and 184,380 available locations. The average radius of available habitat was 568.57 m. We achieved convergence for all hyper-parameters in the model ($\hat{R} \leq 1.1$) and adequate goodness of fit for this model (Bayesian p-value = 0.13). The model estimated the probability of a female using any 30-m X 30-m grid cell on the landscape (prevalence) to be 0.82 (95% credible interval 0.81 – 0.83).

Female white-tailed deer were more likely to use 30-m X 30-m cells on the landscape characterized by deciduous forest cover than any other landscape type before and during the hunting season, while after the hunting season they were equally likely to use deciduous, mixed, and evergreen forest habitat (Table 8, Figure 11). However, as a result of the high prevalence and intercept values female-white tailed deer were highly likely (probability ≥ 0.8) to use deciduous, mixed and evergreen habitats during any time period (Table 8, Figure 11). Females were less likely to use grassland habitats before and during the hunting season than after the hunting season, and this habitat type was also the least likely landscape category to be used before and during the hunting season (Table 8, Figure 11). Females showed no selection for the use of habitats in the other category during any time period.

Female deer were less likely to use 30-m X 30-m cells farther from wooded edges after the hunting season compared to before and during (Table 8, Figure 12a). Females were also more likely to use south facing areas before the hunting season compared to during and after (Table 8, Figure 12b). However, as a result of the large variation in use that exists between deer these two results are hard to observe graphically (Figure 12). Females were more likely to use gentle slopes after the hunting season than before and during (Table 8, Figure 13a), but less likely to use areas closer to roads and with lower road density after the hunting season compared to before and during the hunting season (Table 8, Figure 13b, c). Female deer were consistently more likely to use 30-m X 30-m cells with high contagion values than low contagion values in all periods of the hunting season (Table 8, Figure 13d).

DISCUSSION

Annual survival rates of female white-tailed deer were similar between the 2 study areas, and to other female survival rates observed throughout the Midwest, which range from 0.56 – 0.79 (Nelson and Mech 1986*a*, 1990; Nixon et al. 1991; Van Deelen et al. 1997; Brinkman et al. 2004). Furthermore, consistent with our predictions survival was lowest during the fall (15 September – 15 December), which coincided with the hunting season. In other female white-tailed deer survival studies where antlerless harvest was permitted, hunter harvest was the leading cause of mortality and caused anywhere from 43% – 79% of all mortalities (Fuller 1990, Whitlaw et al. 1998, Hansen and Beringer 2003, Brinkman et al. 2004, Miller 2012). Hunter harvest and wounding loss were the two most common causes of mortality in the GP, causing 46.5% of all mortalities, and the second most common causes in the OZ, causing 38.1% of all mortalities. Determining cause-specific mortality was not an objective in this study, thus resulting in a higher proportion of unknown causes of death than other studies, particularly in the OZ (47.6%). Another important source of mortality for female deer is predation and starvation due to severe winters; however, these mortalities usually only occur when accumulated snow depths are greater than deer chest height and ambient temperatures are consistently $\leq$ -17.7 ^{o}C (Kelsall 1969, Nelson and Mech 1986*b*, DelGiudice et al. 2002). Winter weather was mild in 2016 and 2017 in both study areas (i.e., lowest mean monthly temperature was -9.5^{o}C with no significant accumulation of snow), thus it is not surprising that we did not observe a significant amount of mortality during the winter season (Hansen et al. 1997, Nixon et al. 2001, DelGiudice et al. 2002, Grovenburg et al. 2011*a*).

Contrary to our predictions, yearling and adult females in both study areas increased their movement speeds, and home range sizes during the hunting period, as well as continuously shifted their areas of use throughout the study. Movement speeds and home range sizes were larger in the GP than the OZ, perhaps as a result of the landscape (Walter et al. 2009, Stewart et al. 2011), and adults and yearlings had different home range sizes, but the overall movement trends were similar between the two study areas. This similarity between regions and age classes is surprising given the difference in amount and contiguity of escape cover between the 2 regions (DeYoung and Miller 2011), and the theorized naiveté of yearling deer (Nixon et al. 1991).

Although, since we did not observe a difference in yearling and adult survival rates in either study area, it is possible that yearlings recognized the threat posed by hunters, and altered their behavioral response to hunting pressure in the same way as adults.

In the GP where escape cover is limited and highly fragmented, we expected deer to be more easily disturbed by hunters and therefore increase their movement speeds and be forced to make movements outside of their home range to locate cover (Sparrowe and Springer 1970, VerCauteren and Hyngstrom 1998, Rhoads et al. 2013). This hypothesis was supported by our findings that deer in the GP increased their movement rates and home range sizes during the hunting season, and continuously shifted their space use throughout the study period. However, in the OZ where hiding cover is abundant and less fragmented, we expected deer to be able to move short distances into cover patches, and decrease movements to reduce their susceptibility to harvest (Root et al. 1988, Rhoads et al. 2013, Little et al. 2014), which we did not observe. It is possible that forest habitat in the OZ was not as dense as we suspected, and thus not a suitable source of hiding cover; unfortunately all of our habitat data were remotely sensed so we were not able to measure differences in understory density throughout the OZ region.

We also observed in the GP that as forested cover increased, yearling and adult home range sizes decreased, and deer made slower movements in forested areas compared to non-forested areas. At first these correlations appeared to support our hypothesis that increased forest cover would decrease deer movements during the hunting season. However, if the correlation between home range size and amount of forest cover was related to hunting pressure we expected to see smaller forest dominated home ranges during the hunting season compared to before and after; essentially we would have expected to observe an interaction between forested cover and the hunting period in our home range and movement speed models. In the OZ we similarly observed that deer made slower movements in forested areas compared to non-forested areas, but again this trend was consistent during all periods of the hunting season. In the OZ we also observed that forested cover had no effect on adult home range sizes, but increased forest cover led to increased yearling home range sizes. Yearling deer disperse from their natal home ranges in the early summer (Nixon et al. 1991, DeYoung and Miller 2011) and have been shown to settle in dispersal sinks, or areas where survival past the first fall and winter is unlikely (Nixon et al. 1991). Therefore, it is possible that during their first hunting season yearlings in the OZ occupied forested areas with decreased nutritional quality (i.e., less mast production) or understory density than adults, thus resulting in a need to move farther on the landscape to meet their energetic requirements, or escape from hunters. However, as in the GP, if the correlation between home range size and forest cover was related to hunting pressure we expected to see an interaction between forested cover and hunting season, not forested cover and age.

The risk allocation hypothesis predicts that prey will alter their predator avoidance behaviors in such a way that corresponds to the temporal pattern of risk (Lima and Bednekoff 1999). Therefore, given that hunting was only legal during daylight hours we expected females to alter their crepuscular, diurnal, and nocturnal movement speeds differently during the hunting season compared to before and after (Kilgo et al. 1998, Little et al. 2016, Wiskirchen 2017). For example, Kilgo et al. (1998) found that during the hunting season the nocturnal activity of female deer exceeded their diurnal activity, but not during the non-hunting season, and that diurnal activity during the hunting season tended to be lower than diurnal activity during the non-hunting season. They suggested that females responded to hunting activity by decreasing their diurnal movements to avoid hunters and to compensate for this decrease they increased their nocturnal activity when hunters were not present (Kilgo et al. 1998). In contrast, we observed that crepuscular, nocturnal, and diurnal movement speeds increased by the same amount during the hunting season, and remained elevated following the hunting season. This would suggest that hunters had an effect on deer movement even when they were not present on the landscape (i.e., at night), or that there was some other stimuli influencing deer movements during and after the hunting season.

Average dates of birth were at the end of May 2015 and 2016 in both study areas (Chapter 1); thus, with an average gestation length of 200 days (Verme 1965), peak conception would have been at the beginning of the hunting period in both years. Breeding behavior alters the movement patterns of both female and male deer (DeYoung and Miller 2011), and therefore could be the other factor influencing female movement during this time period (Karns et al. 2012). Competition for mates (Sullivan 2016) and hormonal changes (Ditchkoff 2011) during the rut may cause breeding behaviors to dominate deer behavior until other environmental stimuli reach a certain threshold (Neumann et al. 2009). However, outside of the breeding season females may exhibit more behavioral plasticity to avoid predation, even with a low predation threat (Wiskirchen 2017). In support of this hypothesis, deer in Alabama, where the breeding season and hunting season do not overlap, altered their behavior in response to the hunting season when hunting pressure was at most 0.013 hours of hunting/ha/day (Wiskirchen 2017); other studies, in which the hunting and breeding seasons did overlap, did not see a behavioral response to hunting until hunting pressure exceeded at least 0.390 hours of hunting/ha/day (Autry 1967, Root et al. 1988). While we do not have similar estimates of hunting pressure in either of our study areas, it is possible that the hunting pressure was too low to overcome this threshold, and the alteration in movements we observed was due to biological cues related to breeding (Neumann et al. 2009, Kolodzinski et al. 2010, Karns et al. 2012).

Breeding movements taking precedence over predator avoidance behaviors could explain why females in both study areas, inhabiting different landscapes in terms of habitat composition and fragmentation, similarly increased their movement speeds, home range sizes, and shifted their core areas of use with apparent disregard for the spatio-temporal pattern of predation risk (Neumann et al. 2009, Karns et al. 2012). Female deer have been shown to make movements outside of their home ranges and increase their movement speeds during the rut, presumably to search for prospective mates (Holzenbein and Schwede 1989, Labisky and Fritzen 1998, D'Angelo et al. 2004, Sullivan 2016) or as a result of harassment by males (D'Angelo et al. 2004, Kolodzinski et al. 2010). Female deer have also been shown to increase their probability of activity in both diurnal and nocturnal hours surrounding conception (Sullivan 2016), which would account for the homogeneity in increasing movement speeds we observed throughout the day. Furthermore, the increase in female movements and space use we observed after the hunting season, when the predation threat would have been low, is more easily understood when viewed in a breeding context; Sullivan (2016) found that movement rates of female white-tailed deer in South Carolina were elevated during conception and remained elevated up until 20 days post conception, as compared to movement rates prior to conception.

In both the OZ and GP females did not consistently alter their resource selection in response to the hunting season. In fact, the only resources that were used differently during the hunting season compared to both before and after the hunting season were contagion and woody wetlands in the GP (Figure 8c). Deer in both study areas did show differential use of other resource covariates, such as canopy cover, distance to nearest wooded edge and road density, but deer utilized these resources in a similar way before and during the hunting season, with differential use after the hunting season. The only resource that was used differently before the hunting season compared to during and after was aspect in the OZ (Figure 12b). As discussed previously, it is possible that these shifts in behavior were more related to breeding than hunter avoidance (Neumann et al. 2009). However, it is also possible that changes in resource selection during these time periods were related to forage and nutrient acquisition (Dupke et al. 2017). For example, Cleveland et al. (2012) observed that while increased hunting pressure increased elk movement rates, their resource selection patterns were more influenced by forage related covariates than hunting pressure. Furthermore, Dupke et al. (2017) found that during all seasons, variation in roe deer (*Capreolus capreolus*) resource selection was driven by food as a limiting factor, not lynx (*Lynx lynx*) predation risk.

Temperatures in both study areas steadily declined throughout November and into December, with mean hunting period temperatures ranging from 10.96^{o}C – 13.94^{o}C before the hunting season and 2.97^{o}C – 5.94^{o}C after the hunting season (Prism Climate Group 2018). Winter conditions can have a significant impact on deer resource selection (Jenkins et al. 2007). Although winter weather in our study areas was generally mild, there are still decreased foraging opportunities and lower forage quality in the winter (Torgerson and Porath 1984, VerCauteren and Hygnstrom 2011). The decreased temperatures and reduced amount of daylight after the hunting season may have signaled the onset of winter, causing deer to alter their resource selection after the hunting period to maximize their energy intake (Ditchkoff 2011). It is also possible that these environmental cues, coupled with the end of the breeding season and the decrease in hunting pressure collectively caused deer to alter their use of resources after the hunting season.

In support of this hypothesis deer were more likely to use crop and grassland habitats in the GP, and grassland habitats in the OZ, after the hunting season compared to before and during the hunting season. Both of these habitat types were more open, thus making them a more risky choice during the hunting season (Pilcher and Warmpler 1981, Kilgo et al. 1998). However, these areas can have high nutritional quality (Nixon et al. 1991, Kernohan 1994), therefore making them important in preparation for the winter (Ditchkoff 2011). The continual high likelihood of use of forested areas in the OZ and GP throughout the study is unsurprising given the importance of mast to deer diet in the fall (McCullough 1985, McShea and Schwede 1993). In the OZ females were less likely to use areas farther from wooded edges after the hunting season, but in the GP females exhibited the opposite pattern of use and were less likely to use areas closer to wooded edges after the hunting season. White-tailed deer are thought to prefer edge habitats because of the high diversity of browse and forbs within these areas (Stewart et al. 2011), which can provide high quality nutritional forage for deer. Therefore, our observation that deer were less likely to use edge habitats in the GP is somewhat perplexing. Edges have thought to harbor greater predator densities (Gates and Gysel 1978), but adult deer are unlikely to be predated upon by natural predators in our system (Brinkman et al. 2004). It is possible that interior forest habitats had greater mast availability than edges, but we can’t say that with certainty.

Deer in the GP were also more likely to use south facing slopes after the hunting season, which likely has to do with thermoregulation (Zweifel-Schielly et al. 2009, Barbknecht et al. 2011); south facing slopes are generally warmer than north facing slopes due to increased sunlight. Ungulates have also been hypothesized to use south facing slopes in the winter due to increased forage on these slopes (Sawyer et al. 2007), but given the low elevation in the GP we did not expect this to be the case. In the OZ females were more likely to use areas characterized by gentle slopes after the hunting season compared to before and during the hunting season.

Using steeper slopes during the hunting season could be viewed as an anti-predation strategy as hunters are less likely to use steep slopes (Diefenbach et al. 2005, Keenan 2010). After the hunting season females may have been more likely to use gentle slopes because of the reduced energetic cost of locomotion in flat areas (Hewitt 2011).

Perhaps the most counter-intuitive finding we observed was that female deer in the OZ were less likely to use areas closer to roads, but more likely to use areas with higher road density after the hunting season. We measured road density within a 568.57 m radius of each location, and the probability of use of an area declined precipitously when it was less than 500 m from a road (Figure 13b). Therefore, these findings suggest that when deer were close to roads (i.e., within 0.5 km) they were more likely to use areas with higher road density, but overall they were more likely to use areas greater than 500 m from roads. Ungulate avoidance of roads is well documented (Dyer et al. 2001, Sawyer et al. 2007, Fahrig and Rytwinski 2009), thus making the latter result unsurprising, but does not explain the increased use of areas with higher road densities. Unfortunately we were not able to distinguish between paved and gravel roads, but based on our knowledge of the area gravel roads were more common than paved roads. Therefore, it is possible that areas with higher road density were generally characterized by gravel roads, which received lower amounts of vehicle traffic, while those areas with a lower road density were dominated by paved highways, which had greater amounts of vehicle use. Ungulates have been shown to have a higher tolerance of roads that receive less traffic (Rost and Bailey 1979, Wisdom et al. 2004), which could account for deer use of areas with higher road densities, if those areas were dominated by gravel roads. Furthermore, female ungulates have been shown to be less disturbed by human activity than males (McCorquodale 2003, Montgomery et al. 2012), which could also lead to the increased use of areas with greater road densities.

Ungulates have been found to be more likely to use areas closer to roads at night, when vehicle traffic was reduced (Paton et al. 2017). We did not quantify resource selection differentially depending on the time of day, which could have led to our perplexing results with regards to road density. Similarly, it is also possible females did alter their movements or use of other resources in response to increased hunting pressure, but did so at a smaller spatio-temporal scale than we were able to measure. Sullivan (2016) found that when they did not account for the localized nature of risk surrounding deer stands they saw a uniform increase in use of those areas. However, they found that when they accounted for how many times the stand had been hunted, and how many days it had been since the stand was last hunted, use of the area within 200m of the stand changed (Sullivan 2016). This shows that deer can and do respond to increased hunting pressure, but possibly at a small scale that would be difficult to observe without knowledge of exactly where and when hunters where on the landscape. Because we studied female movements and resource selection at such a large spatial scale (i.e., 8 counties in 2 different regions of Missouri) it was not feasible to obtain such fine scale detail of hunter densities and patterns of use.

MANAGEMENT IMPLCATIONS

Regardless of the exact mechanism driving female deer behavior during this time period we observed that females in different landscapes increased their movement speeds and space use during the hunting season, and altered their resource selection after the hunting period. Many states, including Missouri, purposefully coincide their rifle hunting season with the peak of the breeding season to increase deer vulnerability to increase hunter success and maintain deer populations. We observed that during the November portion of the rifle hunting season that deer increased their movement speeds and areas of use, which could have increased their vulnerability to harvest (Little et al. 2014). However, we did not observe deleteriously low female deer survival during the hunting season, nor did we observe that females in either study area made movements or utilized resources that would prevent them from being harvested. While deer may respond at a small spatio-temporal scale to hunters on the landscape, at a larger temporal and geographic scale, the scale used by managers to make decisions, there do not appear to be any extreme behavioral responses that would affect population management through harvest.

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TABLES

Table 1. Set of candidate models used to determine what factors most influence the movement speed (meters per hour) of female white-tailed deer before, during, and after the November portion of the firearms hunting season in the Glaciated Plains and Ozark regions of Missouri, USA 2015 – 2016.

Model[a,b]	K[c]
Null	3
Age	4
Time of Day	5
Forest	4
Period	5
Time of day × Forest	8
Time of day + Forest + Age	7
Time of day × Age	8
Time of day × Forest + Age	9
Period + Time of day + Forest + Age	9
Period × Time of day	11
Period × Time of day + Forest	12
Period × Time of day + Forest + Age	13
Time of day × Forest + Period	10
Time of day × Age + Period	10
Ownership + Period + Time of day	8
Ownership × Time of day + Period	10
Ownership + Time of day + Period + Forest + Age	10
Ownership × Period + Time of day	10

[a] Age = yearling or adult, time of day = day, night or crepuscular, forest = forested or non-forested location, ownership = public or private land (not included in GP set of models), period = before, during, or after the November portion of the firearms hunting season.

[b] Deer identification was included as a random effect in all models.

[c] Number of parameters.

Table 2. Set of candidate models used to determine what factors most influence the area of female white-tailed deer space use (ha) before, during, and after the November portion of the firearms hunting season in the Glaciated Plains and Ozark Regions of Missouri, USA 2015 – 2016.

Model[a,b]	K[c]
Null	3
Age	4
Forest	4
Ownership	4
Period	5
Age + Forest	5
Age × Forest	6
Ownership + Period	6
Ownership × Period	8
Age + Forest + Ownership + Period	8
Age × Period	8
Age + Period	6
Age × Period + Forest	9
Forest + Period	6
Forest × Period	8
Forest × Period + Age	9
Forest × Age + Period	8
Age × Period + Ownership	9

Forest × Period + Ownership	9

[a] Age = yearling or adult, forest = proportion of home range forested, ownership = proportion of home range that is privately owned (not included in GP set of models), period = before, during, or after the November portion of the firearms hunting season.

[b] Deer identification was included as a random effect in all models.

[c] Number of parameters.

Table 3. Description of the 9 resource attributes assigned to each used and available location included in the resource selection analysis conducted for female white-tailed deer before, during and after the hunting season in the Glaciated Plains and Ozark regions of Missouri, USA, 2015 – 2016.

Covariate	Definition or measurement
Land cover type	Vegetation classes - see table 4
% Canopy cover	0-100%; proportion of 30m cell covered with tree canopy
Distance to edge[a]	Distance (m) from the location to the nearest edge - Distinct transition from a forest to an open area (grassland, cultivated crop, shrub/scrub)
Distance to road	Distance (m) from location to the nearest road
Road density	Length of public roads within 684.12 m (Glaciated Plains) or 568.57m (Ozarks) from the location
Slope	From 0^o (flat) to 45^o
Aspect - north	From -1 (due south) to 1 (due north)
Aspect - east	From -1 (due west) to 1 (due east)
Contagion	Measures the degree to which patch types are aggregated or clumped together; from 0 (every cell is a different patch type) to 100 (landscape consists of a single patch)

[a] Distance to edge was included in the Ozark resource selection model in the pseudo-threshold form of the variable.

Table 4. Description of the land cover types used the resource selection analysis conducted for female white-tailed deer before, during and after the November portion of the firearms season in the Glaciated Plains and Ozark regions of Missouri, USA 2015 – 2016.

Land cover type	Description
Grassland	Areas containing 20% or greater graminoid or herbaceous vegetation. Can be used for grazing or hay production.
Cultivated crop[a]	All land being tilled and/or used for the production of annual crops, such as corn and soybeans, and perennial woody crops. Crop vegetation constitutes > 20% of total vegetation.
Deciduous forest[b]	Areas where 75% of tree species > 5m tall shed their leaves in the fall. Trees make up > 20% of the total vegetation.
Evergreen forest[b]	Areas where 75% of tree species > 5m tall maintain their leaves all year. Trees make up > 20% of the total vegetation.
Mixed forest[b]	Areas where trees make up > 20% of the total vegetation, but neither deciduous nor evergreen trees make up 75% of the total tree cover.
Woody wetlands[a]	Areas where the soil is periodically covered or saturated with water and shrubland vegetation makes up > 20% of the vegetation.
Other	Habitat classes found in the study area that are not one of the above vegetation classes.

[a] Included in other category for resource selection analysis conducted in the Ozark region.

[b] Combined into 1 forest category for resource selection analysis conduction the Glaciated Plains region.

Table 5. Summary of unique female white-tailed deer caught and collared each year in the Glaciated Plains and Ozark eco-regions of Missouri, USA 2015 – 2017. Females marked with Global Positioning Satellite (GPS) collars include fawns (> 6 months old at capture), yearlings, and adults (> 2 years old) caught from December – March of that year. Females marked with Very High Frequency (VHF) collars were caught as neonates in May – June and survived until 15 September of that year and then included in the survival analysis. Numbers in parentheses indicate females caught each year that were included in hunting season behavior analyses.

Study Area	2015		2016		2017	
	GPS	VHF	GPS	VHF	GPS	VHF
Glaciated Plains	30 (23)	9	30 (24)	8	23	9
Ozarks	35 (25)	6	40 (32)	10	26	5

Table 6. Linear mixed models used to evaluate the proportion of space use overlap during the hunting season, ranked according to Akaike's Information Criterion scores corrected for small sample size (AIC_c) and model weights (ω_i) for female white-tailed deer in two study regions in Missouri, USA, 2015 – 2016.

Study Area	Model[a]	AIC_c	ΔAIC_c[b]	ω_i[d]	K[c]
Glaciated Plains	Period	-170.54	0.00	0.42	5
	Age + period	-170.42	0.10	0.40	6
	Null	-166.96	3.56	0.07	3
	Age	-166.79	3.73	0.06	4
	Age × period	-166.28	4.24	0.05	8
Ozark	Period	-165.03	0.00	0.53	5
	Age + period	-164.44	0.60	0.39	6
	Age × period	-161.24	3.79	0.08	8
	Null	-142.23	22.80	0.00	3
	Age	-141.43	23.60	0.00	4

[a] Period is the time period relative to the November portion of the firearms hunting season in Missouri. Before = 11 days before the firearms season began, during = 11 days during the firearms season, after = 11 days after the firearms hunting season. All models contained individual deer ID as a random effect.

[b] Difference in AIC_c relative to the minimum AIC_c

[c] Number of parameters

Table 7. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the case control resource selection model for female white-tailed deer before, during, and after the hunting period in the Glaciated Plains region of Missouri, USA, 2015 – 2016. For each variable [1] represents before the hunting period, [2] the additive effect during the hunting period, and [3] the additive effect after the hunting period. The intercept term includes selection before the hunting season in other habitat.

			95% Credible Interval (CrI)	
Variable	Mean	SD	Lower CrI	Upper CrI
North [1]	-0.11	0.03	-0.16	-0.05
North [2]	0.01	0.04	-0.06	0.09
North [3]	-0.14	0.04	-0.22	-0.07
East [1]	-0.08	0.03	-0.14	-0.03
East [2]	0.01	0.04	-0.06	0.09
East [3]	0.01	0.04	-0.06	0.09
Canopy [1]	1.07	0.11	0.86	1.31
Canopy [2]	0.37	0.16	0.06	0.68
Canopy [3]	0.71	0.23	0.31	1.2
Contagion [1]	-0.14	0.03	-0.21	-0.07
Contagion [2]	0.11	0.04	0.03	0.19
Contagion [3]	-0.03	0.04	-0.11	0.04
Slope [1]	0.17	0.04	0.09	0.24
Slope [2]	0.10	0.05	0.00	0.20
Slope [3]	0.05	0.05	-0.05	0.15

Distance to road [1]	0.22	0.03	0.15	0.29
Distance to road [2]	0.02	0.04	-0.07	0.10
Distance to road [3]	0.04	0.05	-0.04	0.13
Distance to edge [1]	-0.34	0.05	-0.43	-0.24
Distance to edge [2]	-0.16	0.06	-0.28	-0.03
Distance to edge [3]	0.24	0.05	0.14	0.34
Road density [1]	-0.01	0.03	-0.08	0.05
Road density [2]	0.00	0.04	-0.08	0.08
Road density [3]	0.00	0.04	-0.08	0.08
Grassland [1]	0.37	0.11	0.16	0.57
Grassland [2]	-0.11	0.15	-0.40	0.18
Grassland [3]	0.35	0.15	0.06	0.65
Forest [1]	2.28	0.42	1.63	3.27
Forest [2]	0.07	0.50	-0.99	0.96
Forest [3]	0.52	0.92	-0.77	2.97
Woody Wetlands [1]	-0.57	0.24	-1.02	-0.09
Woody Wetlands [2]	-1.16	0.32	-1.80	-0.53
Woody Wetlands [3]	-0.53	0.35	-1.22	0.16
Crop [1]	-0.07	0.10	-0.28	0.13
Crop [2]	-0.28	0.15	-0.57	0.01
Crop [3]	0.31	0.15	0.02	0.61
During	0.20	0.17	-0.14	0.53
After	0.05	0.20	-0.33	0.47

Intercept	0.12	0.15	-0.17	0.42
Prevalence	0.53	0.01	0.51	0.54

Table 8. Mean, standard deviation (SD), lower (2.5%), and upper (97.5%) credible intervals of population level selection parameters for covariates from the case control resource selection model for female white-tailed deer before, during, and after the hunting season in the Ozark region of Missouri, USA, 2015 – 2016. For each variable [1] represents before the hunting period, [2] the additive effect during the hunting period, and [3] the additive effect after the hunting period. The intercept term includes selection before the hunting season in other habitat.

			95% Credible interval (CrI)	
Variable	Mean	SD	Lower CrI	Upper CrI
North [1]	-0.29	0.07	-0.42	-0.16
North [2]	0.31	0.08	0.16	0.46
North [3]	0.34	0.09	0.17	0.51
East [1]	-0.13	0.06	-0.24	-0.01
East [2]	0.06	0.08	-0.09	0.21
East [3]	0.04	0.08	-0.12	0.20
Canopy [1]	-0.29	0.15	-0.58	0.00
Canopy [2]	0.40	0.21	0.00	0.81
Canopy [3]	-0.28	0.25	-0.76	0.22
Contagion [1]	0.52	0.10	0.32	0.73
Contagion [2]	-0.03	0.10	-0.24	0.17
Contagion [3]	0.05	0.11	-0.17	0.27
Slope [1]	0.44	0.08	0.29	0.59
Slope [2]	-0.12	0.09	-0.30	0.06

Slope [3]	-0.29	0.10	-0.48	-0.10
Distance to road [1]	0.14	0.13	-0.11	0.39
Distance to road [2]	0.22	0.14	-0.06	0.51
Distance to road [3]	0.65	0.19	0.28	1.03
Distance to edge[a] [1]	-2.32	0.13	-2.59	-2.07
Distance to edge[a] [2]	-0.25	0.15	-0.53	0.04
Distance to edge[a] [3]	-0.37	0.16	-0.69	-0.05
Road density [1]	1.28	0.14	1.00	1.56
Road density [2]	0.12	0.15	-0.18	0.42
Road density [3]	1.00	0.28	0.46	1.57
Grassland [1]	-1.47	0.41	-2.35	-0.74
Grassland [2]	0.58	0.51	-0.39	1.63
Grassland [3]	1.57	0.54	0.53	2.67
Deciduous [1]	3.06	0.49	2.02	3.98
Deciduous [2]	0.97	0.77	-0.58	2.45
Deciduous [3]	-0.59	0.65	-1.87	0.69
Evergreen [1]	1.22	0.58	0.05	2.33
Evergreen [2]	-0.22	0.76	-1.70	1.29
Evergreen [3]	1.88	0.91	0.05	3.67
Mixed [1]	1.81	1.30	0.12	4.64
Mixed [2]	-0.99	1.45	-4.01	1.27
Mixed [3]	1.68	3.95	-2.18	18.38
During	0.02	0.54	-1.09	1.07

After	-0.75	0.60	-1.92	0.45
Intercept	1.92	0.51	0.99	2.98
Prevalence	0.82	0.01	0.81	0.83

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[a] Distance to nearest wooded edge was included in the model in the pseudo-threshold form of the variable

FIGURES

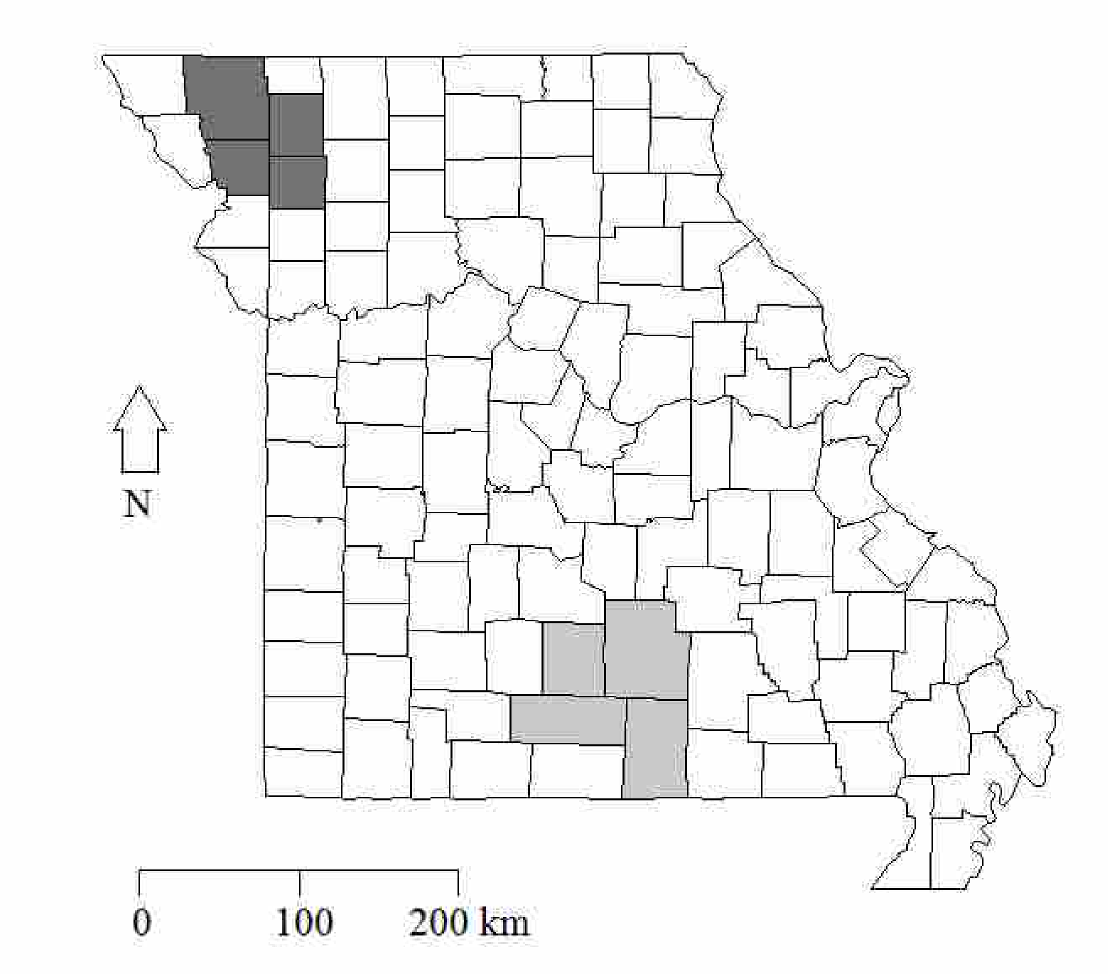

Figure 1. Map of the two study areas in Missouri, USA. The Glaciated Plains study area is shaded in dark grey and the Ozark study area is shaded in light grey.

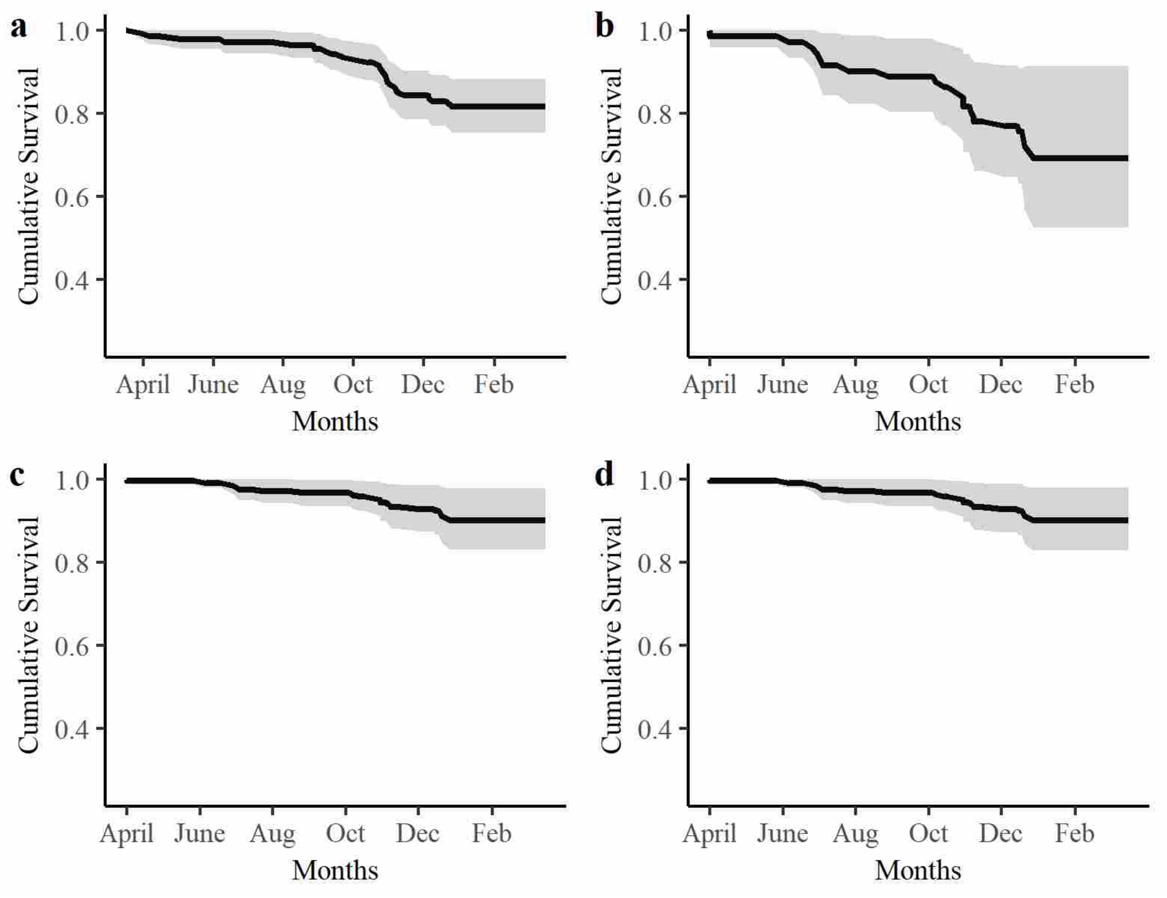

Figure 2. Annual female white-tailed deer survival estimates in two regions of Missouri, USA, using data collected from 1 April 2015 – 31 December 2017. Shaded areas represent 95% confidence intervals. a) Survival curve estimated for females in the Glaciated Plains using the null Cox proportional hazards model. Survival curves estimated for females in the Ozark region using the most supported Cox proportional hazards model, year in (b) 2015, (c) 2016, and (d) 2017.

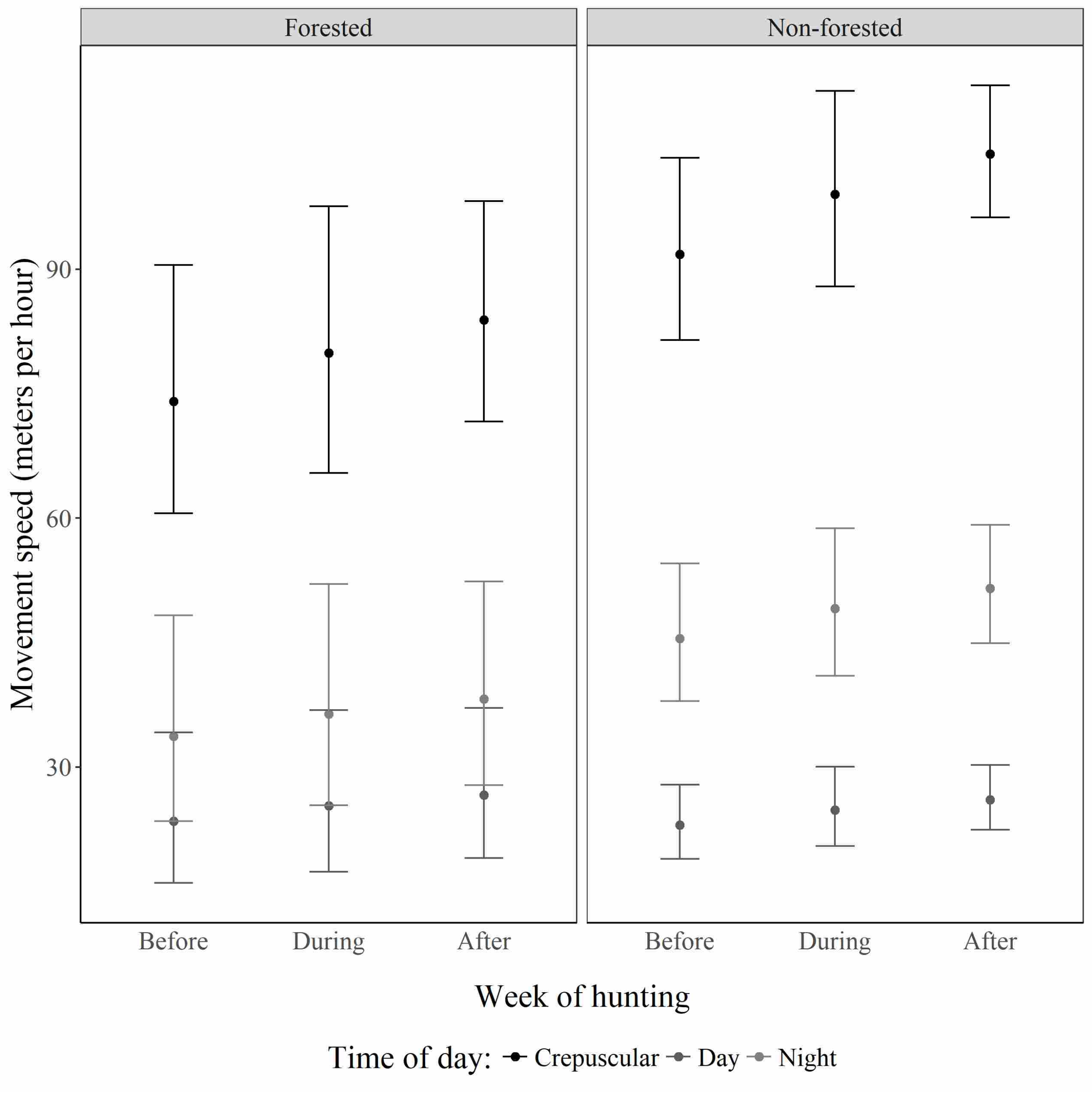

Figure 3. Fitted estimates of female white-tailed deer movement speeds the 11 days before, during, and after the November portion of the rifle hunting season in the Glaciated Plains region of Missouri, USA, 2015 – 2016. Estimates were obtained using the most supported model, time of day × forest + period of hunting, as determined by model selection. Error bars show 95% confidence intervals.

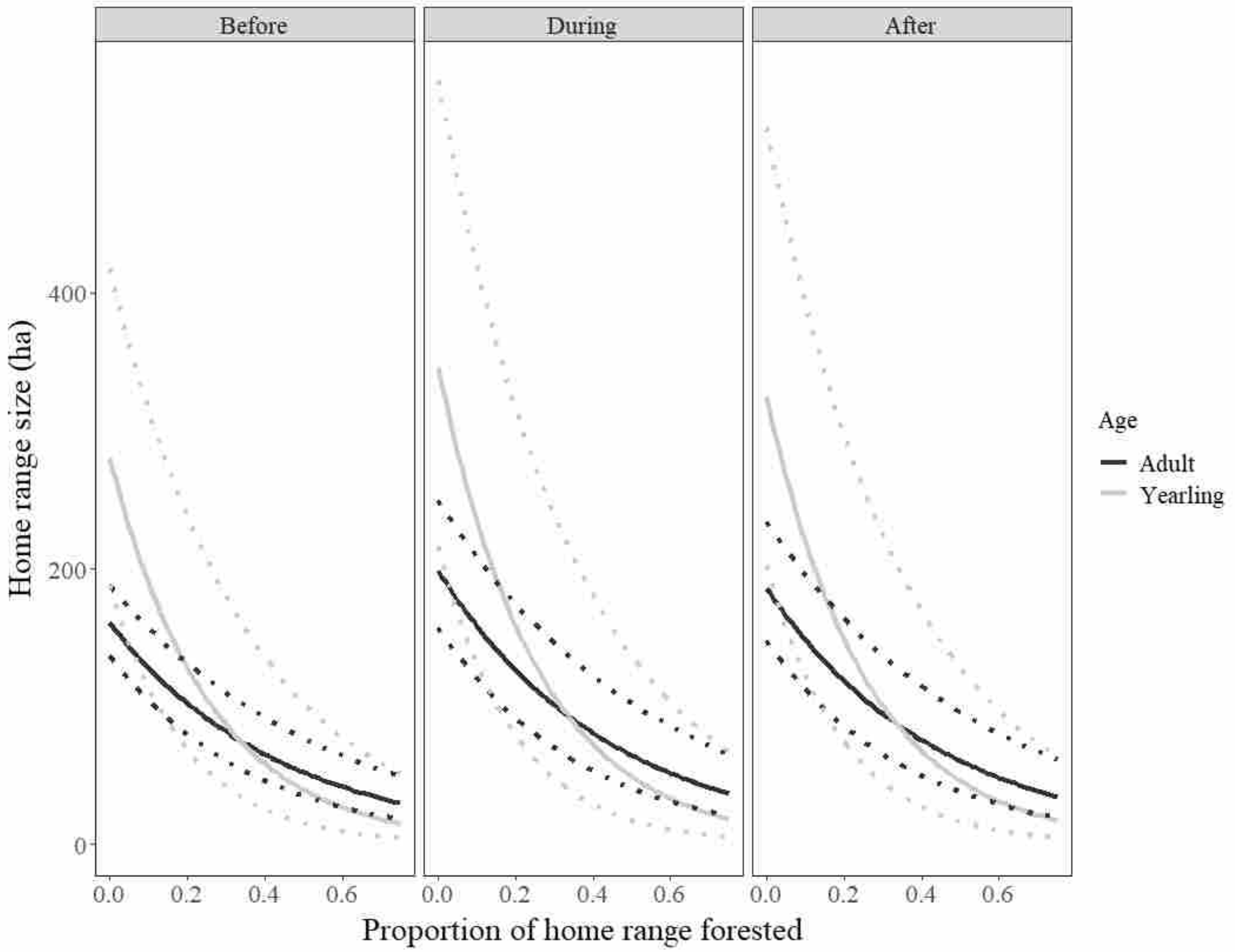

Figure 4. Fitted estimates of female white-tailed deer home range sizes 11 days before, during, and after the November portion of the rifle hunting season in the Glaciated Plains region of Missouri, USA, 2015 – 2016. Estimates were obtained using the most supported model, forest × age + period, as determined by model selection. Dashed lines show ± 1 standard error.

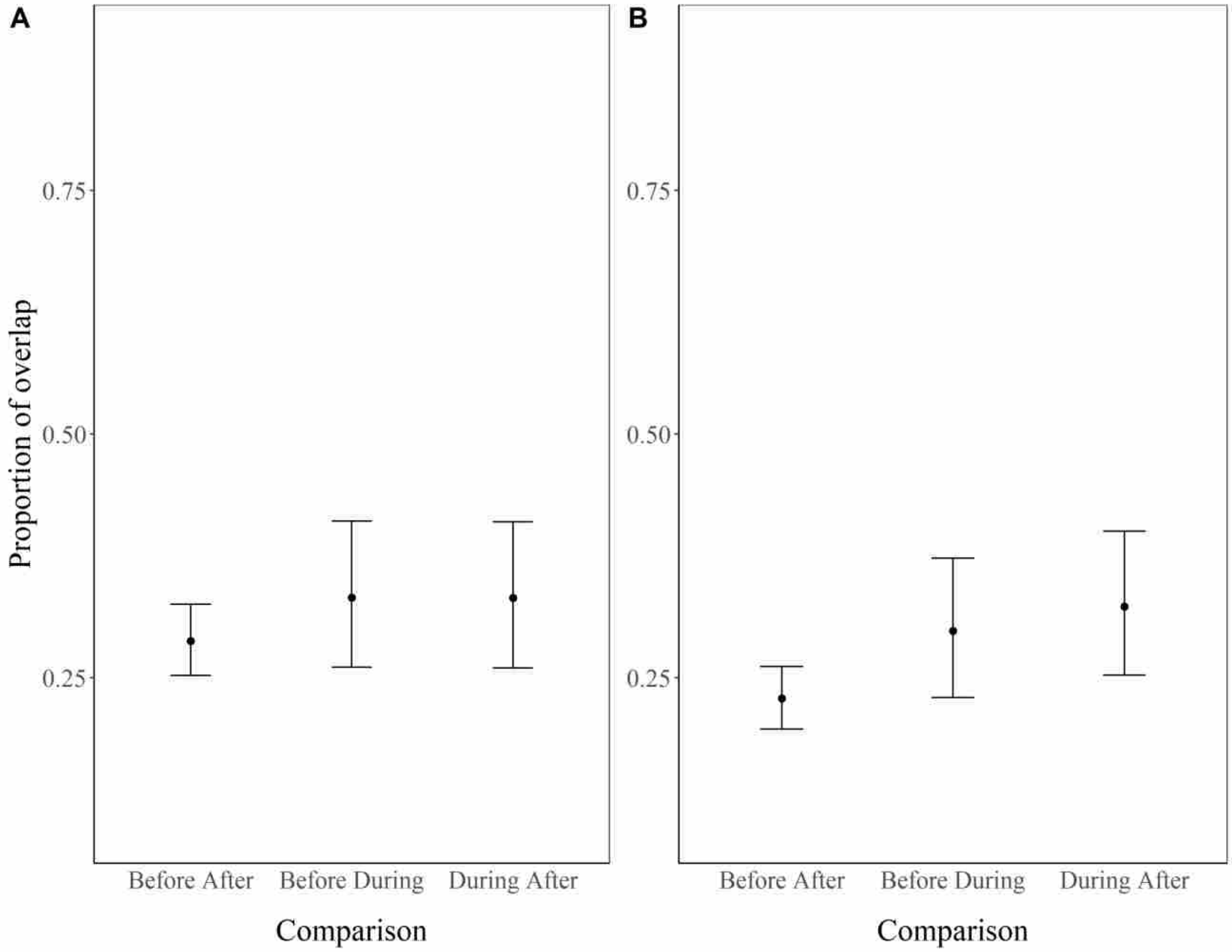

Figure 5. Proportion of space use overlap for female white-tailed 11 days before, during, and after the November portion of the rifle hunting season in Missouri, USA 2015 – 2016. Error bars show 95% confidence intervals. A) Fitted estimates from the top model in the Glaciated Plains region, where comparing the period of hunting was the only covariate. B) Fitted estimates from the top model in the Ozark region, where comparing the period of hunting was the only covariate.

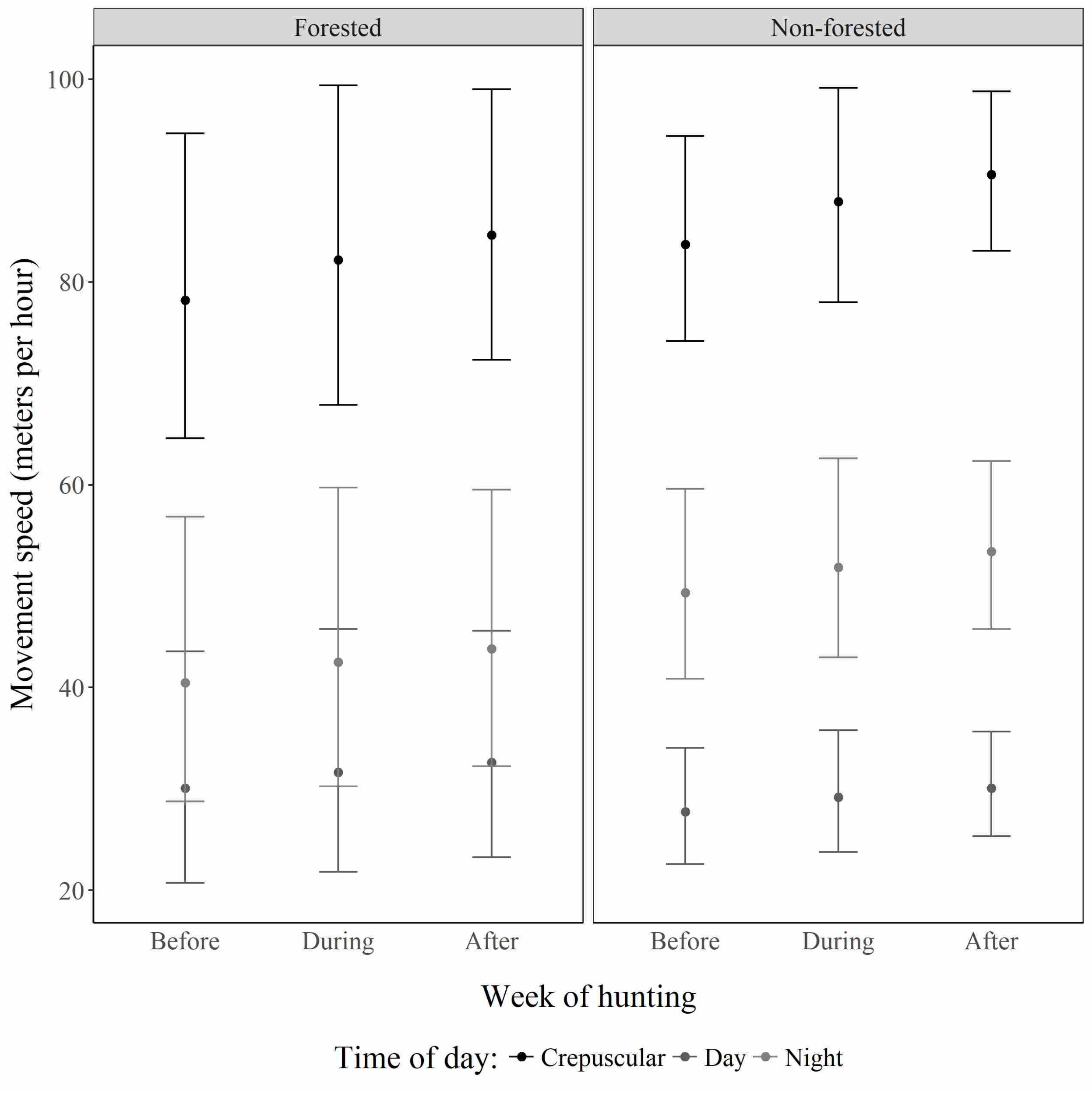

Figure 6. Fitted estimates of female white-tailed deer movement speeds during the 11 days before, during, and after the November portion of the rifle hunting season in the Ozark region of Missouri, USA, 2015 – 2016. Estimates were obtained using the most supported model, time of day × forest + period of hunting, as determined by model selection. Error bars show 95% confidence intervals.

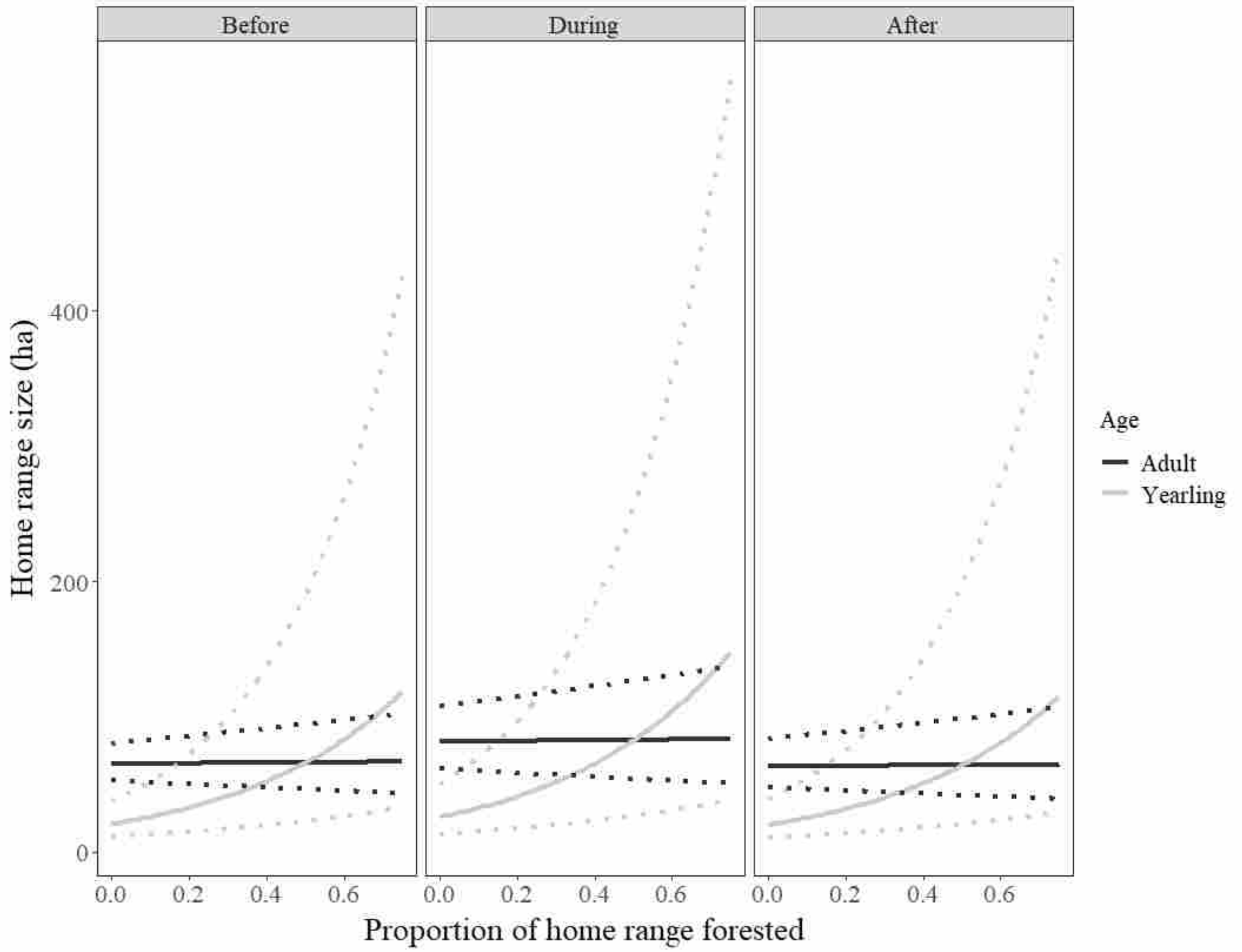

Figure 7. Fitted estimates of female white-tailed deer home range sizes 11 days before, during, and after the November portion of the rifle hunting season in the Ozark region of Missouri, USA, 2015- 2016. Estimates were obtained using the most supported model, forest × age + period, as determined by model selection. Dashed lines show ± 1 standard error.

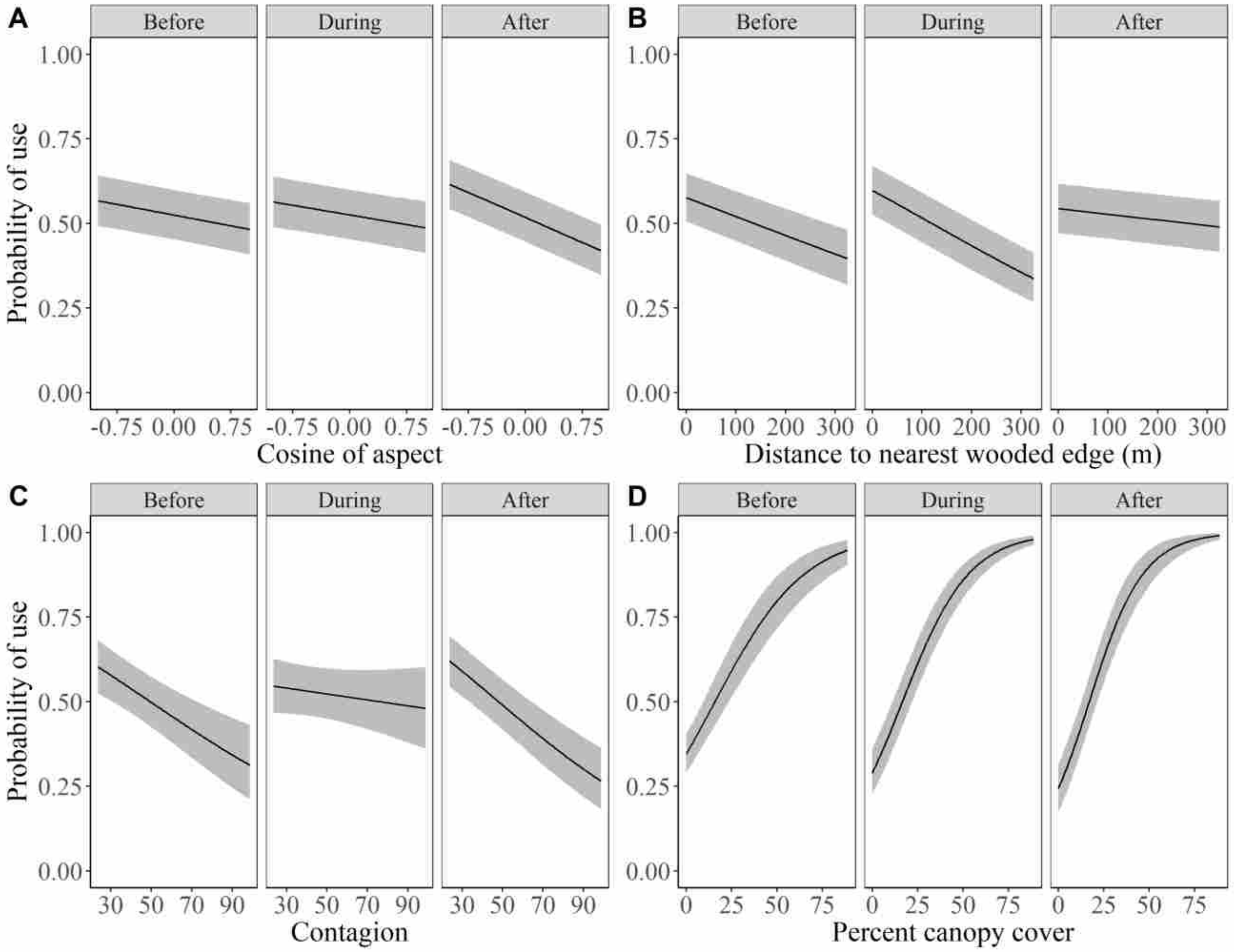

Figure 8. Estimated probability of female white-tailed deer using a 30m X 30m cell before, during, and after the November portion of the rifle hunting season as a function of A) Aspect, B) Distance to wooded edge, C) Contagion, and D) Percent canopy cover, in the Glaciated Plains region of Missouri, USA, 2015 – 2016. Each panel assumes all other continuous variables are fixed at their mean observed value, and use occurs in the other habitat category. The black line represents the mean posterior distribution and gray ribbons represent the 95% credible interval.

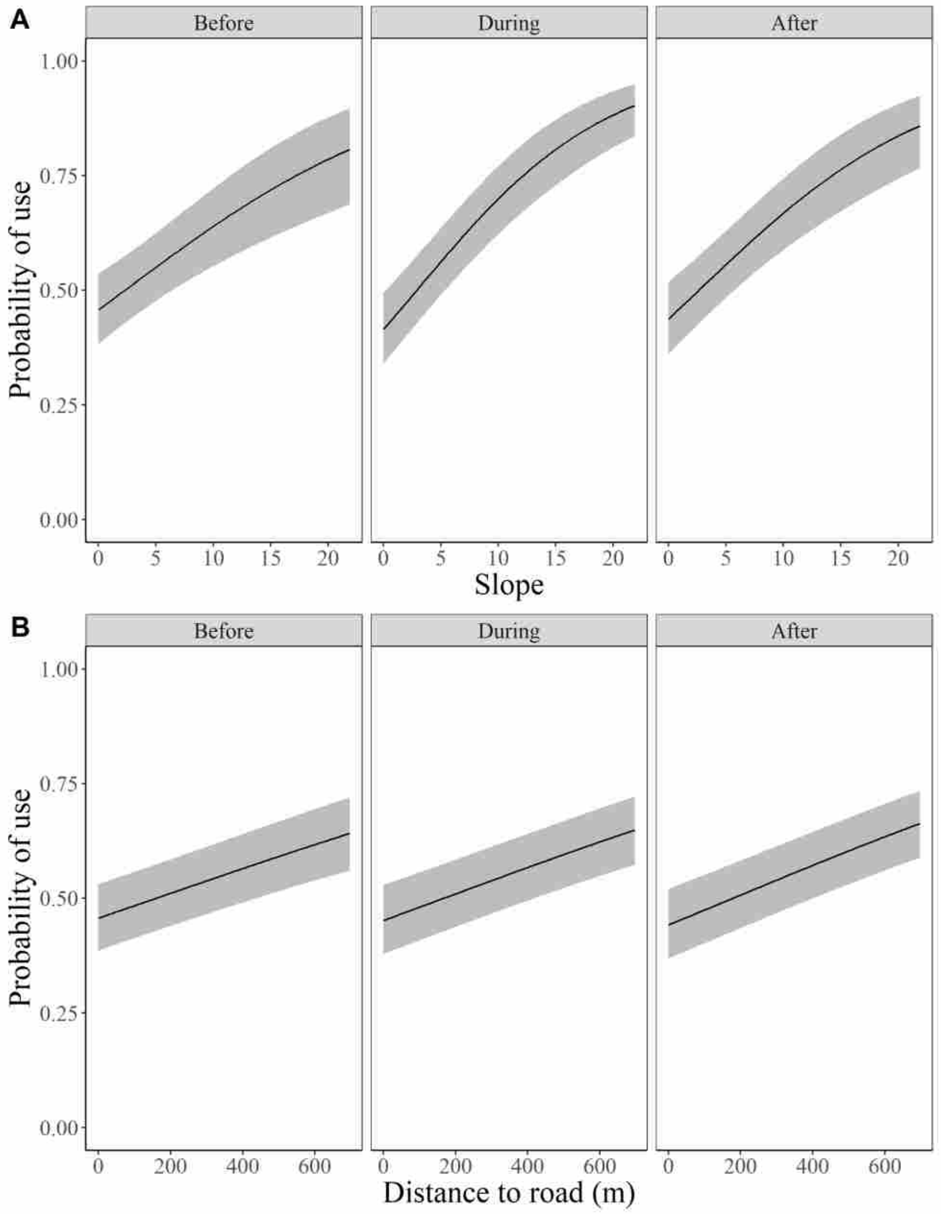

Figure 9. Estimated probability of female white-tailed deer using a 30m X 30m cell before, during, and after the November portion of the rifle hunting season as a function of A) Slope, and B) Distance to nearest road in the Glaciated Plains region of Missouri, USA, 2015 – 2016. Each panel assumes all other continuous variables are fixed at their mean observed value, and use occurs in the other habitat category. The black line represents the mean posterior distribution and gray ribbons represent the 95% credible interval.

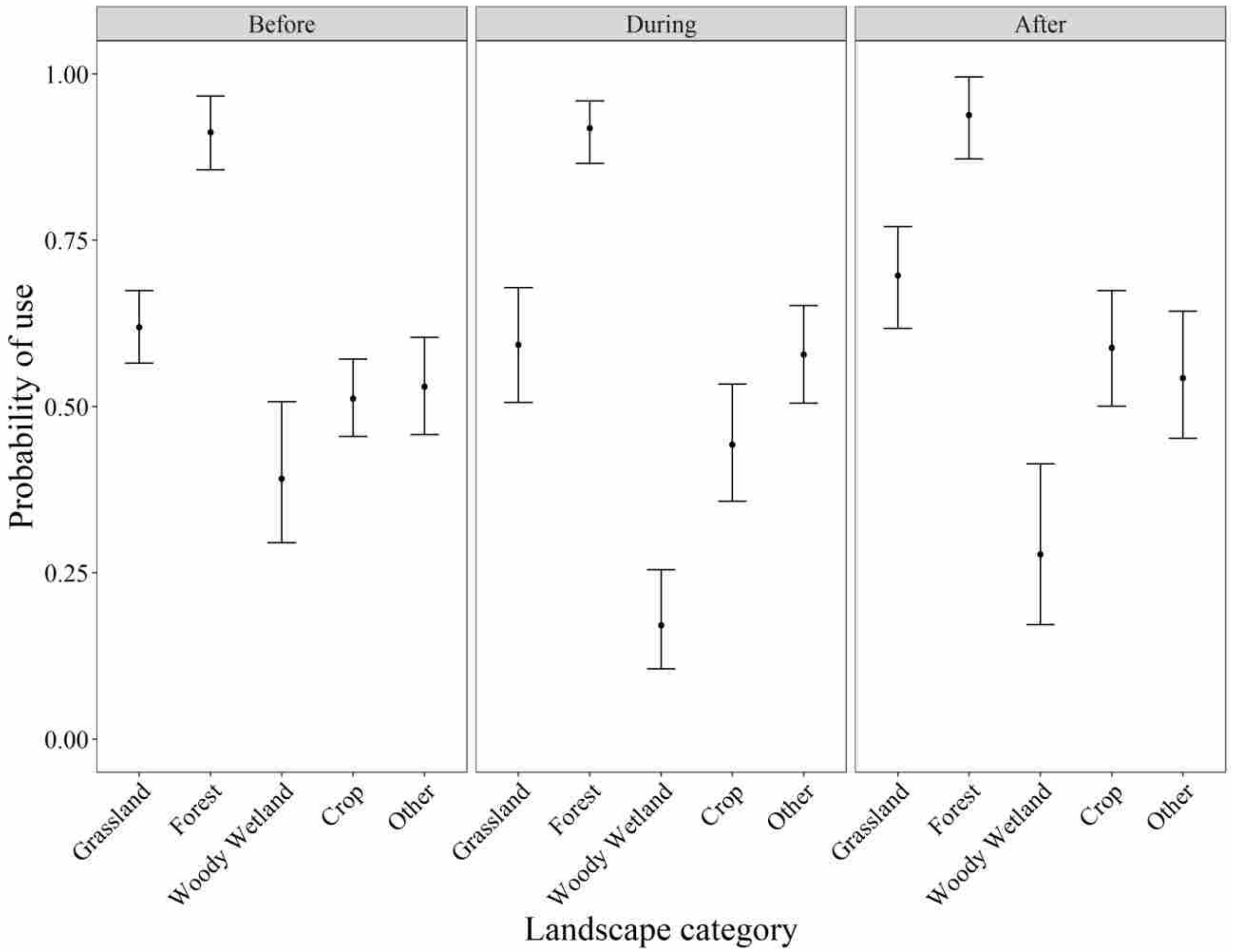

Figure 10. Estimated probability of a female white-tailed deer using a 30m X 30m cell within the landscape as a function of landscape category before, during, and after the November portion of the rifle hunting season in the Glaciated Plains region of Missouri, USA 2015 – 2016. Each panel assumes all continuous variables are fixed at their mean observed values. Circles represent the mean posterior distribution and error bars represent the 95% credible interval.

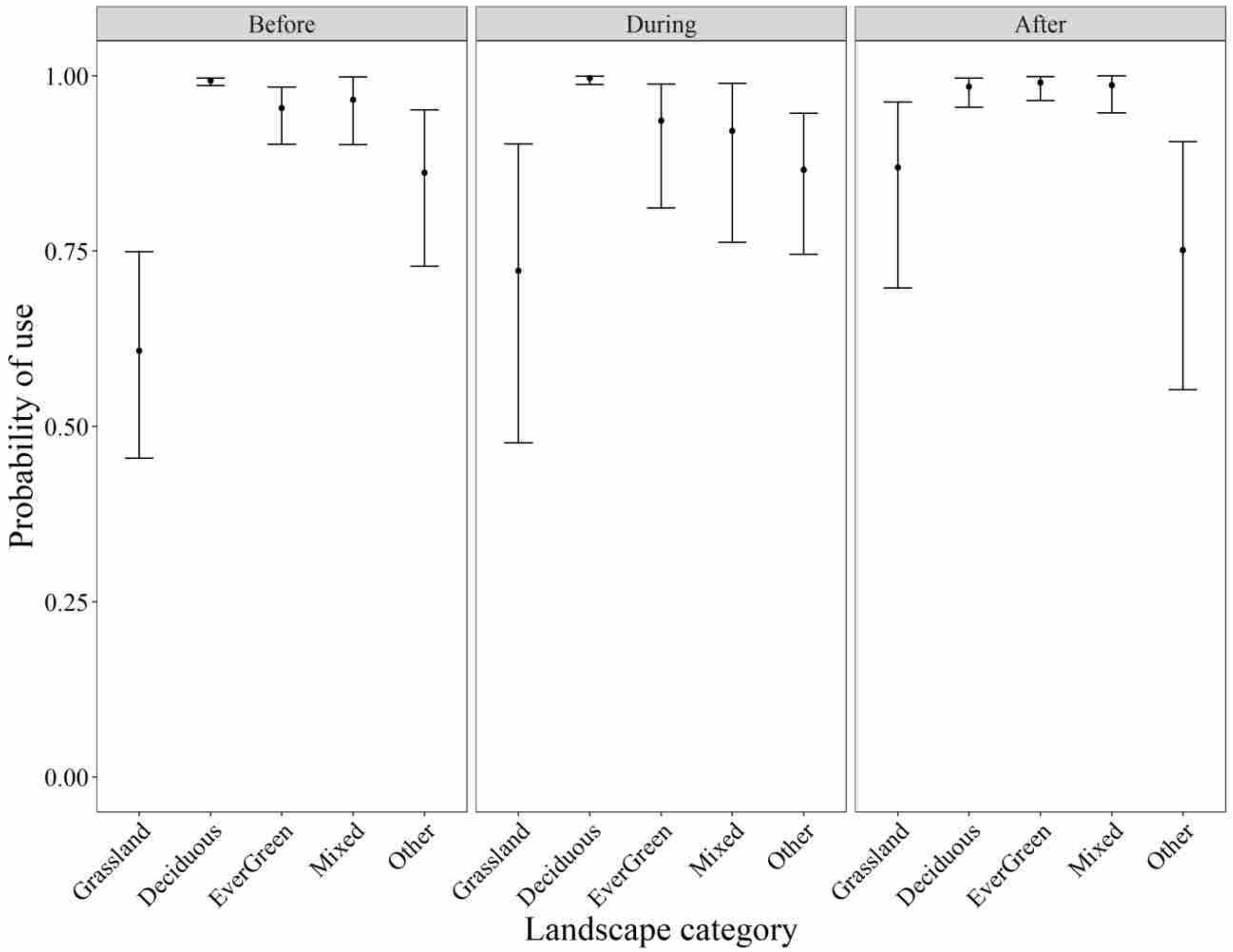

Figure 11. Estimated probability of a female white-tailed deer using a 30m X 30m cell within the landscape as a function of landscape category before, during, and after the hunting season in the Ozark region of Missouri, USA 2015 – 2016. Each panel assumes all continuous variables are fixed at their mean observed values. Circles represent the mean posterior distribution and error bars represent the 95% credible interval.

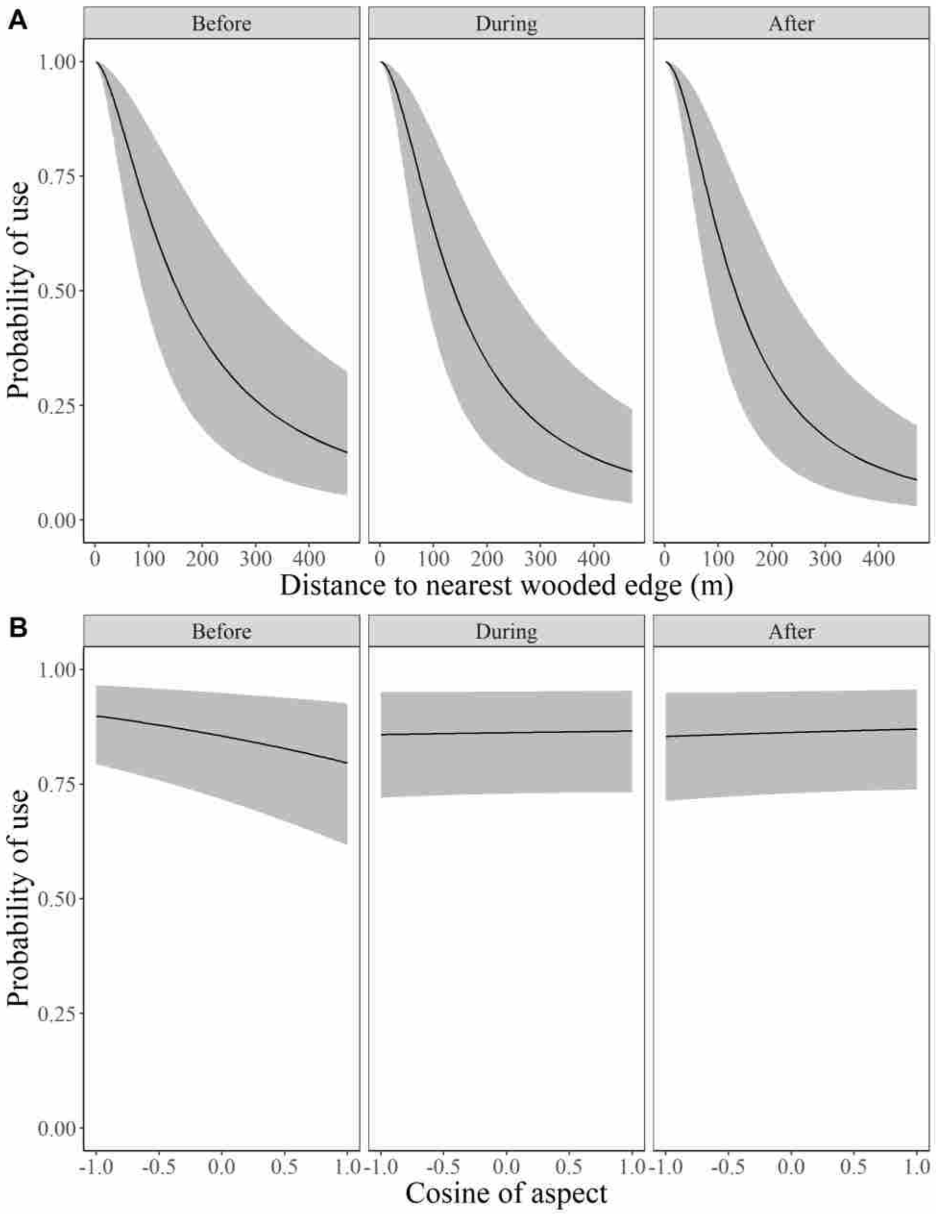

Figure 12. Estimated probability of female white-tailed deer using a 30m X 30m cell before, during, and after the November portion of the rifle hunting season as a function of A) Distance to nearest wooded edge, and B) Aspect in the Ozark region of Missouri, USA, 2015 – 2016. Each panel assumes all other continuous variables are fixed at their mean observed value, and use occurs in the other habitat category. The black line represents the mean posterior distribution and gray ribbons represent the 95% credible interval.

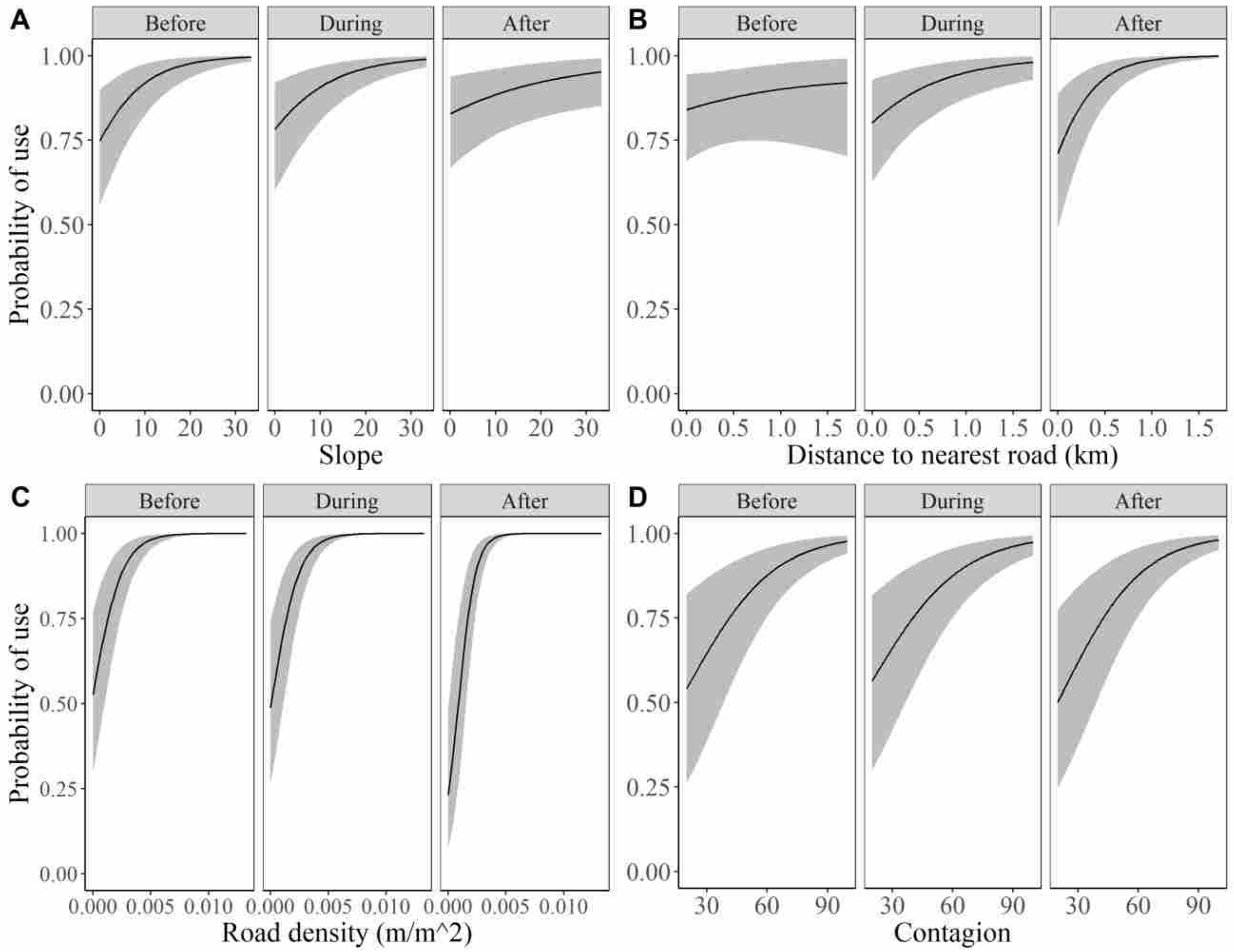

Figure 13. Estimated probability of female white-tailed deer using a 30m X 30m cell before, during, and after the November portion of the rifle hunting season as a function of A) Slope, B) Distance to nearest road (km), C) Road density, and D) Contagion in the Ozark region of Missouri, USA, 2015 – 2016. Road density was measured as the length of roads within a 568.57m radius of a used or available location. Each panel assumes all other continuous variables are fixed at their mean observed value, and use occurs in the other habitat category. The black line represents the mean posterior distribution and gray ribbons represent the 95% credible interval.

APPENDIX A – CALCULATING GPS COLLAR ERROR

METHODS

We tested the accuracy of the 825g Iridium GPS radio-collars (Model G2110E, Advanced Telemetry Systems) by placing collars in locations stratified by percent canopy cover (D'Eon et al. 2002; Di Orio et al. 2003, Lewis et al. 2007) and solar insolation (as a metric of satellite availability and terrain ruggedness; D'Eon et al. 2002, Cain et al. 2005, Lewis et al. 2007). We stratified each study area into open (0%), low, medium, and high canopy cover using the Jenks natural breaks method in ArcGIS 10.3 (Environmental Systems Research Institute Inc., Redlands, California). In the Glaciated Plains (GP) low canopy cover was 1-22% covered by canopy, medium 23-51% and high 51-100%. In the Ozarks (OZ) low canopy cover was 1-34% covered by canopy, medium 35-63% and high 64-100%. The percent canopy cover layer was downloaded from the 2011 US Forest Service National Land Cover Database (NLCD; http://www.mrlc.gov/nlcd11_data.php). Solar insolation was calculated in each study area using the area solar radiation tool in ArcGIS 10.3 using the 30m resolution digital elevation models downloaded from the Missouri Spatial Data Information Service (MSDIS; http://www.msdis.missouri.edu/data/dem/index.html). We stratified each study area in low, medium and high solar insolation again using the Jenks natural breaks method.

We conducted collar testing in June – July 2016 (leaf-on period) and in December 2016 – January 2017 (leaf-off period). We placed collars in all 12 possible combinations of solar insolation and canopy cover, with each combination sampled at two locations within each study area, for 24 test sites per study area per season. The collars were affixed to a post roughly 1m above the ground, with the GPS receiver facing the up. Collars were programmed to record a location every 5 hours and remained at the test site until 2 locations for every hour of the day were collected, which took approximately 10 days. We recorded the actual location of the collar using a high-accuracy handheld GPS unit (Trimble Navigation Ltd., Sunnyvale, California) when the accuracy of the location was <1 m. We used the same model of collar for all tests, and assumed that any variation in accuracy was due to habitat variation (Lewis et al. 2007). We calculated the location error of the collar by determining the Euclidean distance between the actual location and the estimated locations recorded by the collar using the geosphere package (Hijmans et al. 2017) in Program R version 3.4.3 (R Core Team 2017). We pooled all data, across all seasons, habitat types, and study areas to arrive at the mean locational error observed in our study and utilized in our home range analyses. However, we also report differences between study area, canopy cover, and solar insolation, and seasons for future use.

RESULTS

The mean locational error for collars in all locations was 5.92 m (standard deviation [SD] = 9.06 m). The mean locational error across both leaf periods in the GP was 5.76 m (SD = 7.37 m), but 5.05 m (SD = 6.76 m) during the leaf-off period and 6.51 m (SD = 7.89 m) during the leaf-on period. The mean locational error across both leaf periods was 6.08 m (SD = 10.41 m) in the OZ, but 5.43 m (SD = 9.08 m) during the leaf-off period and 6.70 m (SD = 11.72 m) during the leaf-on period. Locational error was greater in areas with higher canopy cover (Table 1), but different levels of solar insolation did not appear to affect locational error (Table 2).

TABLES

Table 1 Estimates of GPS collar error in meters as measured in the Glaciated Plains (GP) and Ozark (OZ) regions of Missouri, stratified by leaf period (off [December 2016 – January 2017] and on [June 2016 – July 2016]), and canopy cover.

Study Area	Leaf Period	Canopy Cover	Mean	Standard Deviation
GP	Off	High	7.67	11.83
GP	Off	Medium	5.70	4.37
GP	Off	Low	3.55	2.02
GP	Off	Open	3.17	1.91
GP	On	High	9.89	9.66
GP	On	Medium	7.79	9.06
GP	On	Low	5.29	6.99
GP	On	Open	3.30	2.00
OZ	Off	High	8.09	14.23
OZ	Off	Medium	7.12	9.60
OZ	Off	Low	3.80	2.45
OZ	Off	Open	3.26	3.89
OZ	On	High	12.47	19.92
OZ	On	Medium	7.71	9.29
OZ	On	Low	3.42	2.30
OZ	On	Open	3.20	2.12

Table 2. Estimates of GPS collar error in meters as measured in the Glaciated Plains (GP) and Ozark (OZ) regions of Missouri, stratified by leaf period (off [December 2016 – January 2017] and on [June 2016 – July 2016]), and solar insolation.

Study Area	Leaf Period	Solar Insolation	Mean	Standard Deviation
GP	Off	High	5.15	9.83
GP	Off	Medium	4.81	4.15
GP	Off	Low	5.18	4.65
GP	On	High	6.28	6.77
GP	On	Medium	7.20	10.41
GP	On	Low	6.01	5.51
OZ	Off	High	6.52	11.18
OZ	Off	Medium	5.73	9.85
OZ	Off	Low	4.10	3.09
OZ	On	High	7.45	16.02
OZ	On	Medium	6.24	10.76
OZ	On	Low	6.42	6.25

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Hijmans, R. J., E. Williams, and C. Vennes. 2017. geosphere: Spherical trigonometry. <https://cran.r-project.org/web/packages/geosphere/index.html>. Accessed 3Feb 2018.

James W. Cain III, Paul R. Krausman, Brian D. Jansen, and John R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. Wildlife Society Bulletin 33:926-934.

Lewis, J. S., J. L. Rachlow, E. O. Garton, and L. A. Vierling. 2007. Effects of habitat on GPS collar performance: using data screening to reduce location error. Journal of Applied Ecology 44:663-671.

R Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>. Accessed 3 Feb 2018.

APPENDIX B – ESTIMATING PREVALENCE AND CASE-CONTROL RESOURCE SELECTION MODEL CODE

METHODS

To obtain an estimate of the probability of a deer using any 30-m X 30-m cell within our 2 study areas for purposes of estimating prevalence, we used remote cameras. Because it was not feasible to place cameras randomly throughout a 15,111.54 km^2 area, we restricted placement of the cameras to areas that could have been used by collared deer. We first created minimum convex polygons (MCP) in ArcGIS 10.3 (Environmental Systems Research Institute Inc., Redlands, California) to obtain a rough estimate of home range size (Kernohan et al. 2001) for 16 randomly chosen deer in each study area, with 4 from each age (sub-adult, adult [≥ 2.5 years of age]) and sex class. We calculated the mean area of the MCP's in each study area, and used these values to obtain radii using the formula Area = $\pi \times \text{radius}^2$. We plotted all of the deer locations collected by the GPS collars in ArcGIS, and used the buffer tool to buffer the locations by the respective radii we calculated (2.00 km in the Glaciated Plains [GP], 1.67 km in the Ozarks [OZ]). We used this buffered area to represent the area that could have been used by collared deer. We then overlaid a grid composed of 30-m X 30-m cells over the buffered area using the fishnet tool. In the center of each of these cells we placed points that were uniquely numbered, which were all the possible camera locations. We downloaded the 2011 land use land cover raster layer from the National Land Cover Database (Homer et al. 2015) and re-classified the 15 land cover types contained in the file into the 4 most common found throughout our study areas: forest, grassland, crop, and other. We used this re-classified layer to assign a land cover type to each possible camera location.

We used a random number generator to choose numbers between 1 – 906, 555 in the GP and 1 – 671,148 in the OZ to randomly place 25 cameras (Bushnell Trophy Cam HD, Bushnell Outdoor Products, Overland Park, KS) within each study area. We stratified the random placement of cameras by habitat and in the GP placed 10 cameras in crop habitat, 9 in grassland, 4 in forest, and 2 in other. In the OZ we placed 2 cameras in crop habitat, 13 in forest, 9 in grassland, and 1 in other. Given that our study areas were ≥ 85% privately owned land we made every effort to place cameras in each randomly chosen location, but if landowners could not be reached, or permission was denied we generated another random location. At each point we placed the camera in a location that was most likely to capture an image of a deer (i.e., on game trails), but only moved the camera at most 21.21 m from the location to ensure the camera was within the 30-m X 30-m grid cell. Cameras were set to take 2 photos when triggered by movement, with a 2 minute delay between each event. We set out 1 round of 25 cameras from November 2015 – March 2016, and a second round from April 2016 – October 2016.

Not all cameras were active the entire time span they were out, so we considered the day they stopped taking pictures as the end date. When going through the photos we recorded the species and number of species of every animal we could identify. To estimate prevalence we calculated the proportion of cameras that detected a deer during a certain time frame. For our estimate of prevalence during the hunting season this included cameras that were active from October – January.

RESULTS

We received data from 48 cameras in the GP, and 44 cameras in the OZ. Cameras took 15,180 and 24,524 pictures in the GP and OZ, respectively, that had a discernable animal in the photo, with 4,270 pictures of deer in the GP and 6,082 pictures of deer in the OZ. From October

– January a total of 16 out of 25 cameras captured an image of at least one deer in the GP, for a prevalence estimate of 0.64. In the OZ a total of 21 out of 25 cameras captured an image of at least one deer from October – January, for a prevalence estimate of 0.84.

LITERATURE CITED

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Kernohan, B. J., R. A. Gitzen, and J. J. Millspaugh. 2001. Analysis of animal space use and movements. Pages 125-166 *in* J. J. Millspaugh, and J. M. Marzluff, editors. Radio Tracking and Animal Populations. Academic Press, San Diego, California, USA.

CASE-CONTROL MODEL CODE

```
model{
 # prior distribution for random intercept

 avg ~ dnorm(0, 0.001)T(-5,5)
  sd ~ dunif(0, 20)
  tau <- 1/(sd^2)

  # prior distribution for fixed effects

  for (j in 1:38){

            a[j] ~ dnorm(0, 0.001)

   }

 # prior distribution for prevalence

  logit_pi ~ dnorm(0.64, 5)
  pi <- ilogit(logit_pi)

  # random intercept for each individual.
```

```
  for (m in 1:nInd){

    b[m] ~ dnorm(avg, tau)

      }

  #For the bayesian p-value
  eta <- n1/(n1 + pi*n0)

# Loop through all observations

  for(i in 1:n){

    #Random intercept and the case control adjustment

    bstar0[i] <- log(((n1) / (pi * n0)) + 1) + b[ind[i]]

    #Process model
    z[i] ~ dbern(psi[i])

    logit(psi[i]) <- bstar0[i] +
      a[1] * north[i] +
      a[2] * north[i] * During[i] +
      a[3] * north[i] * After[i] +
      a[4] * east[i] +
      a[5] * east[i] * During[i] +
      a[6] * east[i]  * After[i] +
      a[7] * canopy[i] +
      a[8] * canopy[i]  * During[i] +
      a[9] * canopy[i] * After[i] +
      a[10] * contagion[i] +
      a[11] * contagion[i] * During[i] +
      a[12] * contagion[i] * After[i] +
      a[13] * slope[i] +
      a[14] * slope[i] * During[i] +
      a[15] * slope[i] * After[i] +
      a[16] * dist_road[i] +
      a[17] * dist_road[i] * During[i] +
      a[18] * dist_road[i] * After[i] +
      a[19] * dist_edge[i] +
      a[20] * dist_edge[i] * During[i] +
      a[21] * dist_edge[i] * After[i] +
      a[22] * dens[i] +
      a[23] * dens[i] * During[i] +
      a[24] * dens[i] * After[i]  +
```

```
    a[25] * Grass[i] +
    a[26] * Grass[i] * During[i] +
    a[27] * Grass[i] * After[i] +
    a[28] * Forest[i] +
    a[29] * Forest[i] * After[i] +
    a[30] * Forest[i] * During[i] +
    a[31] * WoodyWet[i] +
    a[32] * WoodyWet[i] * During[i] +
    a[33] * WoodyWet[i] * After[i] +
    a[34] * Crop[i] +
    a[35] * Crop[i] * During[i] +
    a[36] * Crop[i] * After[i] +
    a[37] * During[i] +
    a[38] * After[i]

  y[i] ~ dbern(mu[i])  # observation model
  mu[i] <- (n1 / (n1 + pi * n0)) * z[i]

  #To calculate the Bayesian p-value

  y_new[i] ~ dbern(mu[i])

  chsq_new[i] <- pow((y_new[i] - psi[i] * eta), 2) /  (psi[i] * eta * (1- psi[i] * eta))
  chsq[i] <- pow((y[i] - psi[i] * eta), 2) /  (psi[i] * eta * (1- psi[i] * eta))

  }

sum_chsq_new <- sum(chsq_new[])
sum_chsq <- sum(chsq[])

}
```