

RESEARCH ARTICLE



Habitat and weather influence body condition in white-tailed deer, Wisconsin, USA

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Abstract

In temperate and northern ecosystems where there are pronounced seasonal patterns in weather and available energy, there are corresponding patterns of body condition among white-tailed deer (*Odocoileus virginianus*). Body condition of white-tailed deer can affect survival and reproduction, which has large repercussions for state-level natural resource agencies that allocate hunting permits. In this study, we investigated how variation in winter weather, spring phenology, habitat composition, and browse quantity affected white-tailed deer body condition across a large spatial scale. Several body condition indicators (e.g., carcass mass, heart fat, antler size) were measured by hunters for 795 deer during September–December 2016–2018 in Wisconsin, USA. Winter severity in the previous year was an unreliable predictor of fall body condition of deer when winters were considered mild or moderate. The timing of spring green-up had a consistent effect on the body condition of all age and sex classes of deer. Earlier spring green-up resulted in heavier fawns and larger antlers among adult males. Region and spring green-up interacted to affect the heart fat of adult females. Earlier springs resulted in adult females in northern and central Wisconsin having a higher probability of heavy heart fat, whereas spring green-up had no effect on adult female heart fat in southern Wisconsin. Effects of habitat differed by age and sex class of deer, and by the body condition metric being evaluated, indicating that there are important physiological differences among age and sex classes of deer that are affected by the environment. Our study demonstrates that the hunting public can contribute



large-scale, cost-effective, and quality data to deer monitoring and research projects. It is important that natural resource agencies be able to identify and recruit highly engaged members of the hunting public to ensure project success. The timing of spring green-up can have lasting effects on deer health that can be consistently observed the following fall, which is in contrast to the effects of winter severity that did not appear to persist when previous winters were mild or moderate. We encourage managers in northern or temperate regions to consider measures of spring green-up timing in conjunction with traditional winter severity when making deer population management decisions, such as antlerless tag allocation.

KEYWORDS

body condition, habitat, health, *Odocoileus virginianus*, spring, weather, white-tailed deer

Ungulate body condition is a function of energy balance and links environmental conditions to population demographics (Parker et al. 2009). Energy balance is reflected in the body condition of individuals, influenced by energetic inputs and outputs, and mediated by weather, land cover, land use, and variation in nutritional quality of forage (Pettorelli et al. 2002, Garroway and Broders 2005, Parker et al. 2009, van Beest and Milner 2013). Poor body condition can lead to lower birth rates (Moyes et al. 2006, Shallow et al. 2015), lower birth mass of neonates (Mech et al. 1991, Duquette et al. 2014, Shallow et al. 2015), lower neonate survival (Duquette et al. 2014), and lower over-winter survival (DelGiudice 1998, Bender et al. 2008). Fluctuations in recruitment and survival as a result of body condition can influence ungulate population dynamics (Post and Stenseth 1998, Patterson and Power 2002, van Beest and Milner 2013).

Among ungulate populations in temperate and northern ecosystems, there are strong seasonal patterns in energy availability and energetic costs (Boyce 1979, Post and Stenseth 1998). The summer growing season is a period of resource abundance when ungulates such as white-tailed deer (*Odocoileus virginianus*; deer) accrue and allocate energy to somatic growth, fat reserves, and lactation (Lesage et al. 2001). Winter, in contrast, is a resource bottleneck for northern deer populations when access to nutritious forage is limited by seasonal plant senescence and snow cover, and the increased cost of thermoregulation and locomotion leads to negative energy balance, and hence reduced somatic and gametic growth and fat reserves (Boyce 1979, Garroway and Broders 2005, Parker et al. 2009). Deer survival is lower during more severe and lengthy winters because deer can exhaust energetic reserves during this time (Nelson and Mech 1986, Hobbs 1989, DelGiudice et al. 2002, Kautz et al. 2020). As such, the effects of winter weather on northern deer populations are often of more concern than summer conditions for deer managers who often use winter severity indices (WSI) to determine winter effects on deer populations (Dittrich 2020).

In addition to weather, the quantity, quality, and spatial distribution of forage and cover can influence seasonal energy balance and body condition (Hobbs 1989, Parker et al. 2009). For example, plants in northern and temperate regions are dormant over winter and experience a period of rapid growth in spring when temperatures warm (Laycock and Price 1970). During early, rapid growth phases, plant tissues contain higher concentrations of nutritious material and lower concentrations of structural and defensive compounds (Mattson 1980, Veraart et al. 2006). The early growth phase of plants in spring is therefore associated with greater benefits per unit foraging time



for ungulates (Demment and Van Soest 1985). Earlier and longer springs should effectively increase the amount of time northern ungulates have access to highly nutritious food through early access and slowed phenological rates of plant development, respectively (Sæther 1985, Nolet et al. 2005). Summer is a period of prolonged forage abundance for deer when food is readily available.

During periods of limited forage resources such as winter, lowland conifer forests are important for some northern deer populations because they provide thermal cover and relief from deep snow (Ozoga and Gysel 1972, Garroway and Broders 2005, DelGiudice et al. 2013). In summer during periods of resource abundance, crop fields, such as those planted to corn, provide important foraging habitats for deer where they occur (Nixon et al. 1991). Thus, deer with access to energy-rich habitat might be hypothesized to have more favorable energy balances compared to deer experiencing similar winter conditions but without such access. The positive effect of habitat with energy-rich forage is likely more apparent when the resource is limited than when it dominates a landscape; thus, there are likely regional differences in which habitat characteristics most strongly influence deer condition.

Multiple measurable carcass attributes provide information about specific body processes of ungulates, and these attributes in conjunction with one another can produce a more complete picture of animal body condition and the overall effect of environmental conditions on animal health (Cook et al. 2001, Taillon et al. 2011). Body mass, for instance, is an integrated measure of skeletal, muscle, and fat mass that also integrates across long-term (i.e., land cover composition and land use) and short-term (seasonal nutritional quality of forage) environmental fluctuations (Lesage et al. 2001, Parker et al. 2009). For instance, regardless of long-term environmental conditions, deer in northern and temperate ecosystems are heaviest in the fall and lightest in spring, reflecting the short-term annual cycling of energy resources among seasons (Nicholson et al. 2008). Fat levels and antler size are affected by short-term environmental conditions such as seasonal resource availability (Mautz 1978, Cook et al. 2004, White et al. 2009), although for antlers, genetics, maternal condition, long-term habitat conditions, and spatial variability in soil nutrients also play a role (Scribner et al. 1989, Monteith et al. 2009).

Among all age and sex classes of deer, fat accumulation and mobilization follow a specific order (Kistner and Trainer 1980). Fat mobilization is such that subcutaneous fat stores are significantly depleted before visceral stores, and bone marrow fat is among the final fat stores to be depleted. Thus, subcutaneous fat is mobilized first and therefore probably more reflective of near-current conditions such as within-season changes in habitat quality, behavior, and physiology (Monteith et al. 2013, Simard et al. 2014). Organ fat, such as heart fat, is not integrated with carcass mass measurements and is acquired before and stored longer than subcutaneous fat. Therefore, organ fat would likely be more reflective of long-term habitat conditions. Carcass mass, as an integrator of subcutaneous fat, muscle, and skeletal mass, likely reflects within-season variation in weather, habitat quality, and behavior more so than internal organ fat, which is not included in carcass mass measurements. Unlike carcass mass and heart fat, antler growth occurs over a more finite period throughout spring to mid-summer but ends before the fall hunting season. As such, antler size could reflect different aspects of the environment than carcass mass or heart fat. For example, energy availability during spring, summer, and fall presumably affects carcass mass and fat levels, whereas fall forage availability would not contribute to antler size because antler growth ceases in late summer.

Most studies of deer nutritional condition are conducted at local spatial scales (Chitwood et al. 2013, DelGiudice et al. 2013, Bergman et al. 2014, Simard et al. 2014), and are thus limited in the gradients of weather, habitat, and forage variables they can assess. By sampling across a large spatial gradient (statewide), researchers can provide information to managers on how environmental variables influence deer body condition appropriate to the management unit of interest (i.e., how winter severity is expected to affect deer condition in a management unit dominated by forest vs. a management unit dominated by cropland).

Our primary objective in this study was to determine the mechanistic links between weather, habitat, browse quantity and quality, and deer body condition. Based on these objectives, we hypothesized that delayed spring green-up and more severe winters would have a negative effect on antler size of adult male deer and fall body condition of all deer; the effects of habitat composition on body condition and antler size would depend on region; body condition would be positively related to the energy available, specifically energy from woody browse; and the

negative effects of winter and delayed spring green-up, and positive effects of habitat quality (i.e., habitat composition and biomass and energy available from woody browse), on body condition would be stronger in juvenile deer than in adult deer.

STUDY AREA

Our study took place during 2016–2018 in Wisconsin, USA (latitude: 42°30'N to 47°05'N, longitude: 86°46'W to 92°54'W), which is located in the Upper Great Lakes region of the midwestern United States (Figure 1). Wisconsin has a land area of 140,663 km² and average elevation of 320 m (range = 176–595 m). There are 4 distinct seasons in Wisconsin with spring generally occurring from March–May, summer occurring from June–August, fall occurring from September–November, and winter occurring from December–February. The climate of Wisconsin is continental, transitioning latitudinally from warm-humid summers in the north to hot-humid summers in the south (Benedetti 2007). Average July temperatures ranged from about 20°C in northern Wisconsin to 22°C in southern Wisconsin and average January temperatures ranged from about –11°C in northern Wisconsin to –7°C in southern Wisconsin (Wisconsin State Climatology Office 2019). Lakes Superior and Michigan modify the climate in adjacent land areas, especially in the lake-effect snowbelt region along Lake Superior where snowfall can exceed 400 cm annually (Benedetti 2007). In contrast, southern Wisconsin receives about 75 cm of snow annually (Benedetti 2007). Wisconsin is geographically diverse, where the Northern Highlands region of northern Wisconsin has larger forests and thousands of glacial lakes, the central part of the state is glacial plain with sandstone and rich farmlands,

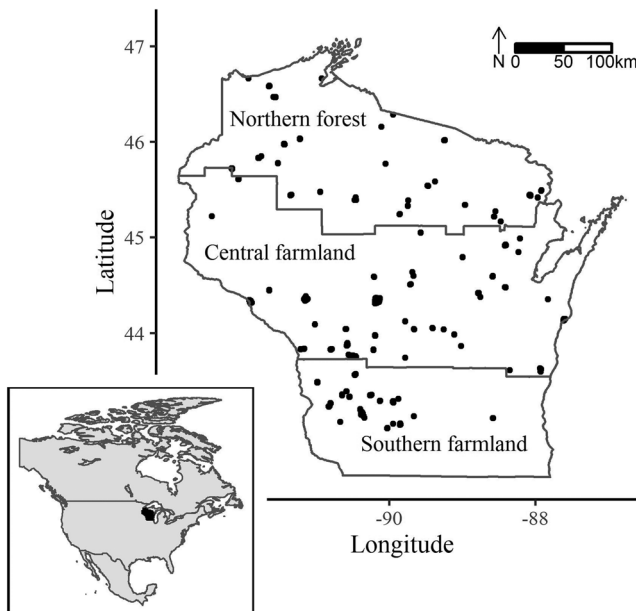


FIGURE 1 Broadly defined regions used for deer management to divide Wisconsin, USA, into tiers from north to south. In the northern forest zone, >50% of the land area in most counties is forested. The central farmland zone transitions from agriculturally dominated landscapes in the south to more forested landscapes in the north. The southern farmland is largely agricultural, with >70% of the land area in some counties in farmland. We used these deer management zones to define regions for habitat characterization and for vegetation sampling. Black dots on the map indicate harvest locations of deer used in this study in 2016–2018. The point distribution reflects the distribution of private properties enrolled in the Deer Management Assistance Program in Wisconsin



and the southwestern part of the state is in the Driftless Area, which was not covered by glaciers in the most recent ice ages and contains many steep hills and bluffs. Land use is predominately agricultural in southern and central Wisconsin, transitioning to recreational and timber land use in northern Wisconsin.

Dominant fauna in Wisconsin includes deer and their predators. Deer range across the entire state, whereas larger predators such as gray wolves (*Canis lupus*) and American black bears (*Ursus americanus*) have core ranges mainly in the northern two-thirds of the state. Smaller predators such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) also range statewide. Deer hunting zones in Wisconsin generally follow borders between major ecotones, which facilitates the use of various deer harvest and management approaches across a diverse landscape with different habitat characteristics, weather patterns, ownerships, land uses, and deer population sizes. The northern forest zone encompasses the Superior Lowlands and Northern Highlands geographic regions (Wisconsin Department of Natural Resources 2015) and had over-winter deer densities that ranged from 3.5 deer/km² to 12.7 deer/km² in 2018 (Wisconsin Department of Natural Resources 2018). Northern Wisconsin is dominated by the maple-beech-birch cover type, which is largely composed of sugar maple (*Acer saccharum*), red maple (*Acer rubrum*), paper birch (*Betula papyrifera*), and American beech (*Fagus grandifolia*). The central farmland zone encompasses the Central Plains geographic region (Wisconsin Department of Natural Resources 2015) and is transitional between agriculture-dominated landscapes to the south and mainly northern hardwoods and coniferous forests to the north. Over-winter deer densities in the central farmland zone ranged from 5 deer/km² to 22 deer/km² in 2018 (Wisconsin Department of Natural Resources 2018). The Western Uplands and Eastern Ridges and Lowlands geographic regions compose the southern farmland zone, which is heavily agricultural and contains major metropolitan areas such as Milwaukee and Madison (Wisconsin Department of Natural Resources 2015). Over-winter deer densities in the southern farmland zone ranged from 1 deer/km² (in the Milwaukee Metro Area) to 21 deer/km² in 2018 (Wisconsin Department of Natural Resources 2018). Southern Wisconsin is largely dominated by an oak-hickory cover type, with dominate tree species comprising white oak (*Quercus alba*), red oak (*Quercus rubra*), bitternut hickory (*Carya cordiformis*), shagbark hickory (*Carya ovata*), red pine (*Pinus resinosa*), black walnut (*Juglans nigra*), and jack pine (*Pinus banksiana*).

METHODS

Deer body condition

Options for carcass condition evaluations include the Kistner scoring index (Kistner and Trainer 1980) and the modified Kistner scoring index (Cook et al. 2001), which measures body fat at several deposition sites and involves assigning a rank score. A kidney fat index is a measure of a single ratio of kidney mass and kidney fat mass (Riney 1955, Finger et al. 1981). Other options such as measuring rump fat thickness (Stephenson et al. 1998) or quantifying total body fat involve either specialized field equipment like portable ultrasound machines or whole carcasses and laboratory methods (Stephenson et al. 1998, Cook et al. 2001). Each option listed above requires either extensive training, specialized equipment, or both. For our study, we relied on landowners enrolled in Wisconsin's Deer Management Assistance Program (DMAP; i.e., hunters), a program administered by the Wisconsin Department of Natural Resources (WDNR), to collect body condition data from deer during fall 2016, 2017, and 2018. Providing specialized training or equipment to hunters collecting deer data for us across the state was not feasible. Therefore, we developed a protocol similar to the modified Kistner scoring system where field-based measurements of deer body condition were easy to accurately collect with minimal training and minimal equipment. Measurements we asked hunters to make were also measurements many of them make each year for their own records, such as carcass mass and antler scores.

Prior to fall hunting seasons, we provided hunters with in-person and online training options to learn the data collection procedure. Hunters also received sampling kits that contained all necessary materials for data collection including protocols, nitrile gloves, datasheets, property maps, tape measures, scales for measuring carcass mass,



coin envelopes for teeth, markers, laminated photo-framing sheets, universal secure digital memory cards, and postage-paid return envelopes for submitting data. Hunters assigned a deer identification number to each deer shot on their property and marked the harvest location on property maps. Body condition measurements included body length (from the tip of the nose to the base of the tail where it met the body), hind leg length (from tip of the hoof to the hock), chest girth (at the broadest point directly behind the front shoulders) and field-dressed carcass mass (including hide and antlers). Male deer antler measurements included the number of legal antler points (points > 2.54 cm), inside spread (distance between main beams at the widest point), and basal circumferences of right and left main beams. Hunters extracted a lower incisor to submit for aging via cementum annuli (Gilbert 1966). Photographs submitted by hunters of the head of the deer, from the front, aided in sex and age determination if the appropriate fields were not completed on the datasheets.

Hunters photographed hearts, first wiping them of debris and blood and centering them on laminated white sheets with the coronary groove facing outward. Hunters submitted heart photos via email or by mailing us the memory card included in kits. Two WDNR biologists visually quantified organ fat from heart photos. Biologists independently considered the width and opaqueness of fat along the top of the heart and along the coronary groove, fat extension along the coronary groove, and the presence or absence of fat at the bottom tip of the heart (Kistner and Trainer 1980). Four categories of heart fat were possible: heavy, moderate, slight, or no fat. Biologists compared their independent heart rankings and conferred with each other to come to a consensus when there was disagreement. Biologists did not classify heart fat if photos were of poor quality (e.g., blurry, grainy, black and white printed photos) or if fat was obscured because of damage from bullets or handling by hunters.

We determined ages by analysis of cementum annuli, or by visual confirmation using head photos for fawns, for 84% of deer. We could not determine ages for the remaining 16% of deer because we were unable to accurately determine age of young deer (yearlings) using cementum annuli, the tooth sample was damaged, or a tooth or head photo was not submitted. We removed from analyses deer that lacked age data. Of the 795 deer submitted to the study, a subset came from the 43 properties where we were able to collect vegetation data, leaving us with a sample size of 494 (Appendix A, available in Supporting Information) deer that could be used in statistical models to examine direct links between deer body condition and vegetation components of their neighborhoods.

Weather, habitat, and vegetation data

We georeferenced harvest locations recorded on hunter property maps using ArcGIS (ArcMap 10.6.1, Esri, Redlands, CA, USA) and created a 15-km² circular buffer around each harvest location, which was approximately double the area of an annual deer home range (~7.5 km²) in Wisconsin (J. J. Dittich, WDNR, unpublished data). Buffered areas represented a neighborhood in which the deer likely lived. We chose the 15-km² buffer size for several reasons. First, the locations at harvest relative to home range centers and boundaries were unknown because deer were not being tracked with tags or radio-collars prior to harvest. A circular buffer double the size of an average home range was likely to encompass a larger portion of the normal home range. Second, we extracted remotely sensed data from within the buffered area around each harvest location, which allowed us to quantify land cover, weather, and browse quality indices that could be directly linked to body condition of each deer.

Weather

We obtained daily minimum and maximum temperatures throughout winter and spring, and daily snow depths in winter, from several weather observation networks across Wisconsin including WDNR weather stations (J. J. Dittich, unpublished data), National Oceanic and Atmospheric Administration Remote Automatic Weather Stations (Western Regional Climate Center 2018), National Weather Service (NWS) weather stations, the Cooperative



Observer Daily Climate Network, and the NWS-Federal Aviation Administration Hourly Airport Network. We used weather station temperature and snow depth data to calculate the annual WSI for the winter prior to harvest and winter prior to birth, and to estimate the beginning, length, and end of the spring green-up period for the spring prior to harvest.

The WSI is calculated annually in Wisconsin between 1 December and 30 April (Kohn 1975). A value of 1 is awarded to any day when the minimum temperature is $\leq -17.78^{\circ}\text{C}$ and an additional value of 1 is awarded to any day when snow depth is ≥ 45.72 cm. Zero, 1, or 2 points can be awarded each day and the points accumulate over winter to produce the annual WSI value, which is used to classify the harshness of a particular winter. The WDNR considers winters to be mild when annual WSI values are ≤ 50 , moderate if values are between 50–79, severe if values are between 80–100, and very severe if values are > 100 .

We developed an index of spring green-up using annual growing degree days (GDD) with red maple phenological threshold values for flowering as a proxy for the start and end of the spring green-up period. The GDD is a measure of heat accumulation using daily minimum and maximum ambient air temperatures and is strongly correlated with phenological stages in plant development (Aber et al. 1996). We calculated GDD values daily using the same network of weather stations used to calculate annual WSI values. We then used known GDD threshold values associated with specific red maple phenological stages to estimate the date red maple began flowering, the length of the red maple flowering period, and the date red maples finished flowering.

The daily GDD is calculated by:

$$\text{GDD} = \frac{T_{\max} + T_{\min}}{2} - T_{\text{base}}, \quad (1)$$

where $T_{\max}$ is the daily maximum temperature, $T_{\min}$ is the daily minimum temperature, and T_{base} is a threshold temperature, which for red maple is 10°C (University of Massachusetts [UMASS] Extension 2019). Daily values are accumulated throughout spring. Red maple phenological events are closely correlated with GDD (UMASS Extension 2019). Additionally, red maple is the most common and widely distributed tree regenerating in the understory throughout Wisconsin (Nowacki et al. 1990, Palik and Pregitzer 1992, Abrams 1998, Kurtz et al. 2015). Red maple begins flowering relatively early (Hutnik and Yawney 1961) and is commonly browsed by deer (Williamson and Hirth 1985, Hughes and Fahey 1991, Abrams 1998). Red maple is a reliable indicator of spring green-up and a potentially biologically relevant forage for deer in Wisconsin during the spring flush of nutrients. Red maples begin blooming when cumulative GDD values reach about 49, and typically finish blooming when cumulative GDD values reach about 99 (UMASS Extension 2019). We assumed that red maples began flowering on the date when GDD reached 49 and stopped flowering on the date when GDD reached 99. The spring green-up period was the number of days between the estimated start date and the estimated end date of flowering.

We generated annual WSI and spring green-up maps with post-processed weather station data using spatial interpolation with ordinary kriging (Lefohn et al. 2005) in package automap (Heimstra et al. 2008) in program R (version 3.5.0; R Core Team 2018). The spatial extent of the maps covered the state of Wisconsin and the raster resolution was 30×30 m. We overlaid deer neighborhoods on WSI and spring green-up maps and extracted average values from within each neighborhood. Additionally, we extracted birth year WSI values by overlaying deer neighborhoods on WSI maps for the year deer were born.

Habitat

We created a land cover dataset by merging remotely sensed data from 2 sources: the Wisland 2 land cover dataset that was produced in 2016 (Wisconsin Department of Natural Resources 2016) and the Cropland Data Layer (CDL), which is produced annually (U.S. Department of Agriculture National Agricultural Statistics Service 2018). Wisland 2 is a raster dataset with ground resolution of 30 m, derived from satellite imagery from the



Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper, and the Landsat 8 Operational Land Imager. We merged the CDL and Wiscland 2 data layers to create unique land cover surfaces for each year of the study that reflected changes in crop rotation and different crops being planted from one year to the next. We overlaid the CDL layer onto the Wiscland 2 layer and let the CDL replace Wiscland 2 cover types where the CDL indicated agricultural lands were present. After combining the remotely sensed datasets, we used literature review and expert knowledge to reclassify cover types to better represent biological relevance for deer in Wisconsin. The reclassification used a combination of level 2 and level 3 from the hierarchical Wiscland 2 cover types and level 4 row crop and pasture and grasses cover types from the CDL dataset. We classified human developments on the landscape as having either low or medium development. Forested cover types included upland coniferous, aspen (*Populus* spp.), oak (*Quercus* spp.), and hardwood forests. We included cattails (*Typha* spp.) as a cover type because they can serve as important cover in parts of Wisconsin where agriculture is the dominant land use and there is little forested area. The row crops cover type mainly consisted of corn, alfalfa, and soybeans, which are major crops grown in Wisconsin; however, lesser grown row crops were also included in the row crop category. The pastures and grasses category included warm and cool season grasses and all pastures. A null cover type included areas not used by deer such as open water, emergent wetlands, and highly developed areas. We superimposed deer neighborhoods on the final land cover surface and extracted land cover type values for each pixel, and the total number of pixels available within each neighborhood to calculate the proportion of each cover type per neighborhood.

Vegetation biomass and energy from woody browse species

To index the woody browse biomass available within deer neighborhoods, we employed a stepwise approach. Initially we identified 9 common tree species or genera to create the index value of woody browse quantity and quality. Those species included red oak, white oak, birch (*Betula* spp.), aspen, cherry (*Prunus* spp.), basswood (*Tilia americana*), red maple, sugar maple, and ash (*Fraxinus* spp.). We selected these species because they were frequently browsed by deer in Wisconsin, had economic timber value, or both. These 9 species are also being recorded across Wisconsin as part of a larger effort to monitor forest regeneration. We opportunistically sampled those 9 species from public lands in each forest type in each region of Wisconsin. We identified stems to species and classified them into 4 height classes: ≥ 5 –35 cm, > 35 –91 cm, > 91 –152 cm, and > 152 –183 cm. We clipped each living twig on the stem at a 3-mm diameter, the average bite diameter at the point of browsing on trees by deer (Windels and Jordan 2008). We separated leaves and twigs into summer and winter browse components, respectively, then bagged and dried them in an oven at 45°C until they were mass stable. Finally, we recorded dry mass of the leaves and twigs by species and height class for each forest type in each region of Wisconsin.

We sent dry samples to the University of Wisconsin Soil and Forage Lab (Marshfield, WI) for chemical analysis to determine percent neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin, cellulose, hemicellulose, and crude protein. We used these values to determine the digestible and indigestible components of the samples to calculate available energy. To calculate available energy from digestible components of plants, we used samples collected between 1 July and 15 August and employed the total digestible nutrients (TDN) equation:

$$\text{TDN} = 96.35 - (\% \text{ADF} \times 1.15), \quad (2)$$

where the %ADF is the percent of indigestible fiber in each plant (Jayanegara et al. 2019). The TDN is the sum of the digestible fiber, protein, lipids, and carbohydrates in a plant. We then calculated available energy:

$$\text{Available energy (kcal) per stem} = (\text{TDN} \times 4.5) \times \text{dry biomass}, \quad (3)$$



where TDN in each sample is multiplied by the value 4.5, which is the typical number of calories/gram of woody browse (gross energy; Berteaux et al. 1998). Using equation 3 we quantified the energy available/stem for each woody browse species.

To determine stem density on properties, we randomly selected 3–8 locations within each forest cover type on each property. We generated random locations prior to site visits using ArcMap. At each random location, we established a circular plot with a 2.07-m radius. Within each plot we identified stems to species or genera and classified by the same height class sampled for woody nutrition. We calculated the average number of stems within a plot for species and genera across plots and scaled to stems/ha. We then multiplied stems/ha by the number of hectares for each forest type within a neighborhood. To estimate the amount of biomass and energy available within plots, we coupled stem biomass and energy values for each species with stem density estimates for each species. We used biomass/stem for each species to calculate the overall browse biomass/ha and browse biomass/neighborhood. We used the TDN and biomass estimates for each species to estimate the overall available energy from browse index species within each neighborhood.

We used the proportion of forested land in each deer neighborhood and the biomass index and total energy index from woody browse species to calculate energy values for each deer neighborhood. We used energy residuals from a simple regression of biomass or energy values as a function of the proportion of forested land in the deer neighborhood as an index of available forage quality. Positive residuals values indicated that higher than expected biomass or energy from woody browse was present given the proportion of forest land within neighborhoods, whereas negative residuals values indicated that lower than expected amounts of biomass or energy from woody browse was available given the proportion of forest land within neighborhoods.

Statistical analyses

We divided our dataset into fawns (<1.0 yr; $n = 101$), adult females (≥ 1.5 yr; $n = 246$), and adult males (≥ 1.5 yr; $n = 147$; Appendix A). There are age- and sex-specific life-history and reproductive traits that vary among northern ungulates, supporting this division of data (Mitchell et al. 1976, Simard et al. 2014). We used carcass mass and heart fat as response variables for each age and sex class. Basal circumference of the main beams and inside spread of antlers were additional response variables specific to adult males. We tested for correlation among response variables with Kruskal-Wallis tests. We fit generalized linear mixed regression models using the lme4 package (Bates et al. 2015) in program R (version 3.5.0; R Core Team 2018) to carcass mass and antler size response variables. Heart fat was a categorical and ordinal response variable, so we used a cumulative link mixed regression model with the ordinal package (Christensen 2019) in program R to fit models. We included a property identifier as a random effect in all models because of likely autocorrelation among deer harvested on the same properties.

We identified 19 explanatory variables to assess the variation in body condition. The base model included age, region (deer management zone), and harvest date; weather variables included birth year WSI, WSI, start of green-up, end of green-up, and green-up period; habitat variables included row crops, pasture and grass, oak, aspen, conifer, hardwoods, and cattails; food variables included browse quantity, energy, biomass residuals, and energy residuals; and property of harvest was a random effect in all models. We determined multicollinearity between explanatory variables using a variance inflation factor (VIF) correlation test from package car (Fox and Weisberg 2019) in program R. We considered variables with VIF values ≥ 5 to be collinear (Lewis et al. 2007) and we did not include them in the same candidate models. Correlated variables included the spring green-up metrics (start, end, and period of green-up). Biomass and energy, and biomass and energy residuals were not included in the same models with each other and were not included in models with forested cover types because we calculated their values using forest proportions. We included harvest date as a fixed effect in all models because deer were harvested between 15 September and 1 January each year. We also included region as a fixed effect in all models and an age as a fixed effect in all adult models.



To select the best model for each age- and sex-specific group, and for each response variable, we followed an iterative procedure with 4 distinct steps, similar to Simard et al. (2014) and the model selection procedure proposed by Hosmer and Lemeshow (2002). Because of the large number of potential combinations of parameters, we did not include all combinations at each step. Rather, we constructed candidate model sets with combinations of parameters that we considered biologically likely to affect deer body condition. At each step in the procedure, we selected the best model using Akaike's Information Criterion (AIC; Burnham and Anderson 2002), where the best model had the lowest AIC value. We considered models with $\Delta\text{AIC} < 2$ equivalent to the best model. From these equivalent models, we selected the most parsimonious model with the fewest parameters.

The first candidate model set included unique combinations of non-collinear variables with no interaction terms and no nonlinear terms (Appendix B). We used the best model from step 1 as a reference model in subsequent steps. In step 2 we added a layer of complexity to the reference model by including potential nonlinear terms (step 2a) or potential interaction terms (step 2b) when we felt there was reasonable ecological justification. In step 3 we used the reference model and top models in steps 2a and 2b to construct a final candidate model set that included interaction terms and nonlinear terms, if identified in step 2.

We calculated the marginal R^2 (R^2_m fixed effect) and conditional R^2 (R^2_c fixed and random effect) for final generalized linear models using package MuMIn (Barton 2019) in program R. We performed a k-fold cross validation using 5 folds with 70% of the data used for the training set and 30% of the data held out and used as the test set for each iteration (Roberts et al. 2017). We used the average values for root mean squared error (RMSE), mean squared error (MSE), mean absolute error (MAE), and R^2 to evaluate model accuracy. We ran Lipsitz test and Pulkstensis-Robinson chi-squared and deviance tests to determine the goodness of fit for the top ordinal regression models (Fagerland and Hosmer 2016) using package generalhoslem (Jay 2019) in program R.

RESULTS

Hunters submitted an average of 5 deer/property during fall hunting seasons of 2016 ($n = 56$), 2017 ($n = 281$), and 2018 ($n = 458$) for 795 deer submitted to the study. The median age of female deer was 3.5 years old (range = fawn–15.5 yr), and 69% of female deer were ≤ 3.5 years old. The median age of male deer was 2.5 years old (range = fawn–8.5 yr), and 72% of male deer were ≤ 2.5 years old (Appendix A).

We did not detect a difference in carcass mass between male and female fawns ($F < 0.001$, $P = 0.99$, $R^2 = -0.02$), whereas among older age classes, males weighed more than females ($F = 58.04$, $P < 0.001$, $R^2 = 0.26$). Body mass increased with age for adult males and adult females ($H_7 = 82.61$, $P < 0.001$; $H_{13} = 39.94$, $P < 0.001$, respectively) until males reached approximately 5–6 years old and until females reached about 3–4 years old, after which time carcass mass remained relatively stable with increasing age. Heart fat was not significantly correlated with carcass mass among fawns ($H_2 = 2.92$, $P = 0.23$). Males and females had similar amounts of heart fat (McFadden's pseudo $R^2 = 0.01$) and for males and females, heart fat was not significantly correlated with age ($H_2 = 3.16$, $P = 0.21$; $H_2 = 1.16$, $P = 0.56$) or carcass mass ($H_2 = 3.10$, $P = 0.21$; $H_2 = 4.20$, $P = 0.12$, respectively).

For antler characteristics of adult males, inside spread and basal circumference were positively correlated ($F = 299.4$, $R^2 = 0.70$, $P < 0.001$). Inside spread and basal circumference were correlated with age ($H_7 = 84.073$, $P < 0.001$; $H_7 = 80.46$, $P < 0.001$, respectively). Inside spread and basal circumference were also positively correlated with carcass mass ($F = 179.0$, $R^2 = 0.58$, $P < 0.001$; $F = 177.7$, $R^2 = 0.59$, $P < 0.001$, respectively). But neither inside spread nor basal circumferences were significantly correlated with heart fat ($H_2 = 2.73$, $P = 0.26$; $H_2 = 5.82$, $P = 0.54$, respectively).

The average winter severity value during the study was 23.6 ± 0.4 (SE), and annual average WSI values were 14.1 ± 0.7 in 2016, 15.5 ± 0.5 in 2017, and 29.4 ± 0.4 in 2018. Each winter during the study was considered mild, on average, and only 4 individual deer experienced winter WSI conditions that would have been considered moderate. The average spring green-up date occurred earliest in 2016 on 28 March ± 2 days,



whereas the average spring green-up date occurred on 7 April $\pm$ 0.3 days in 2017 and on 26 April $\pm$ 0.1 days in 2018. The proportion of deer neighborhoods with row crops and pasture or grass varied by region, where in northern Wisconsin the average proportion of a deer neighborhood in row crops and pasture or grass was $1.8 \pm 0.3\%$ and $3.4 \pm 0.4\%$, respectively, whereas row crops and pasture or grass accounted for $18.3 \pm 1.2\%$ and $7.6 \pm 0.4\%$, respectively, of neighborhoods in central Wisconsin and $27.3 \pm 0.9\%$ and $16.1 \pm 0.5\%$, respectively, of neighborhoods in southern Wisconsin. The proportion of different forest types in deer neighborhoods also varied by region. The average proportion of each deer neighborhood in conifer was $23.0 \pm 1.2\%$ in northern Wisconsin, $3.2 \pm 0.4\%$ in central Wisconsin, and $1.7 \pm 0.3\%$ in southern Wisconsin. Hardwoods accounted for $20.3 \pm 2.1\%$, $27.1 \pm 1.3\%$, and $39.4 \pm 1.1\%$ of neighborhoods in northern, central, and southern Wisconsin, respectively. Oak forests accounted for $27.4 \pm 2.5\%$, $14.4 \pm 1.1\%$, and $11.5 \pm 0.8\%$ of neighborhoods in northern, central, and southern Wisconsin, respectively.

Body condition versus environment

Carcass mass

Harvest date, WSI, green-up start date, row crops, pasture and grasses, aspen, conifer, hardwoods, cattails, and an interaction between region and oak forests were parameters included in the top model explaining fawn carcass mass (partial R^2 ; Table 1). Cross-validation scores for the top model of fawn carcass mass indicated only moderate fit and predictive ability ($R^2 = 0.35$, $MSE = 22.94$, $RMSE = 4.79$, $MAE = 3.99$). We determined the following mass estimates for each model parameter by holding all other model parameters at their means. During fall hunting season, fawn carcass mass increased from an expected average of 23.59 ± 0.98 kg on 21 September (ordinal day 265) to 32.57 ± 1.80 kg on 29 December (ordinal day 363), an average gain of 0.11 kg/day (Figure 2A). The expected average fall carcass mass of fawns decreased from 38.38 kg when spring green-up began early (ordinal day 63) to an expected average carcass mass of 27.12 kg when spring green-up began late (ordinal day 120; Figure 2B). Expected average fawn carcass mass in fall increased from 26.83 kg to an expected average mass of 35.49 kg as WSI during the previous winter increased from a minimum value of 8 to a maximum value of 46 (Figure 2C). The minimum percentage of hardwoods forests in neighborhoods was 3%, which resulted in an expected average fawn carcass mass of 22.11 kg. Fawn carcasses were heavier in neighborhoods with a higher percentage of hardwoods forests, reaching an expected average carcass mass of 38.10 kg when the percentage of hardwoods forests in neighborhoods was at a maximum of 76% (Figure 2D). Fawn carcasses were heavier in neighborhoods with more pasture and grasses, reaching an expected average of 33.11 kg when the proportion of pasture and grasses in neighborhoods was at maximum of 31% (Figure 2E), whereas in neighborhoods with 0% pasture and grasses, the expected average fawn carcass mass was 27.89 kg. Expected fawn carcass mass also increased curvilinearly with increasing percentage of row crops within neighborhoods, from a 30-kg minimum average carcass mass when 0% row crops were available to a 40-kg maximum average carcass mass when row crops were at a maximum of 60% of neighborhoods (Figure 2F). As the percentage of oak forests within neighborhoods increased from a minimum of 0% to a maximum of 44% in northern Wisconsin, expected average fawn carcass mass increased from an expected average mass of 26.68 kg to an expected average mass of 44.91 kg. Similarly, in central Wisconsin expected fawn carcass mass increased from a minimum expected mass of 26.68 kg to a maximum expected mass of 60.45 kg as the percentage of oak forests within neighborhoods increased from a minimum of 0% to a maximum of 58%. Fawn carcass mass did not vary significantly in response to the percentage of oak forests within neighborhoods in southern Wisconsin (Figure 2G). The percentages of cattails, aspen, and conifer did not significantly affect fawn carcass mass in any region (Table 1).

Age, harvest date, the percentage of oak forest within neighborhoods, and an interaction between region and the percentage of hardwoods forests within neighborhoods were parameters included in the best model of adult



TABLE 1 Coefficient values for independent variables in the top models for white-tailed deer fawn, adult female, and adult male carcass mass. Deer were harvested by hunters from across Wisconsin, USA, 2016–2018. Est. = estimate, SE = standard error, t = t -value, P = P -value, p . R^2 = partial R^2 , WSI = winter severity index

Independent variables	Fawn carcass mass (kg)				Female carcass mass (kg)				Male carcass mass (kg)			
	Est.	SE	t	P	Est.	SE	t	P	Est.	SE	t	P
Intercept	29.33	0.85	34.57	<0.001	51.20	0.86	59.89	<0.001	102.61	3.04	23.87	<0.001
Age					1.45	0.42	3.46	<0.001				
Harvest date	1.94	0.46	4.22	<0.001	1.33	0.48	2.79	0.01	−3.12	0.73	−4.25	<0.001
WSI	1.85	0.94	1.96	0.05					0.73	0.89	0.82	0.42
Start green-up	−2.19	0.85	−2.58	0.01								
Hardwoods	3.98	1.24	3.20	<0.001								
Ecoregion North × oak	4.74	1.62	2.93	0.01								
Ecoregion Central × oak	4.79	1.40	3.43	<0.001								
Ecoregion South × oak	1.57	1.40	1.12	0.27								
Row crops ²	1.12	0.44	2.52	0.01					2.52	1.25	2.01	0.05
Pasture grass	1.66	0.83	2.00	0.05								
Cattails	0.88	0.60	1.48	0.14								
Aspen	−0.68	0.83	−0.82	0.42								
Conifer	−0.18	0.90	−0.20	0.84								
Oak					−1.65	0.73	−2.24	0.02				
Ecoregion North × hardwoods					−0.15	2.84	−0.05	0.96				
Ecoregion Central × hardwoods					−2.49	1.01	−2.46	0.02				
Ecoregion South × hardwoods					0.05	0.95	0.05	0.96				
Age ^{−0.5}									−46.79	4.62	−10.12	<0.001
Ecoregion North									3.04	3.93	0.77	0.45
Ecoregion South									−5.91	3.16	−1.87	0.08
Row crops									3.56	1.33	2.68	0.01

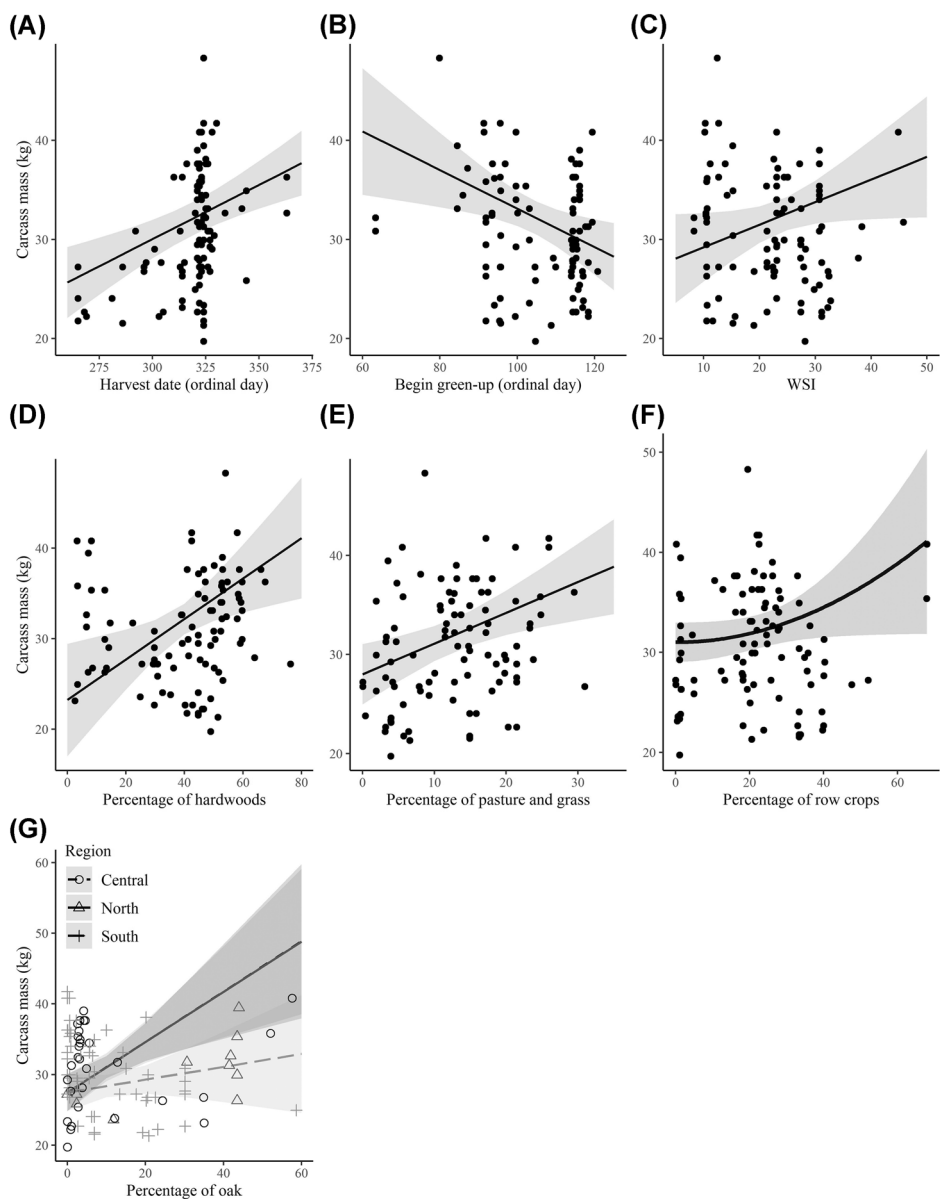


FIGURE 2 Fixed effects of parameters with significant effects on white-tailed deer fawn carcass mass from the top model, selected by iterative process and Akaike's Information Criterion. Fawns were harvested in Wisconsin, USA, 2016–2018. The winter severity index (WSI) is an indicator of how severe the prior winter was, using snow depth and minimum daily temperature values. Fawns harvested later in the fall hunting season had greater mass than fawns harvested earlier in the hunting season (A), had less mass when spring green-up was later (B), and had greater mass if the winter prior had been more severe (C). Fawns also had greater mass with a higher percentage of hardwoods forests (D), pasture and grasses (E), and row crops (F) in their neighborhoods. Fawns in northern and central Wisconsin had greater mass when the percentage of oak in their neighborhoods was large, whereas the percentage of oak forests in southern Wisconsin (light gray dashed line) had no significant effect on fawn carcass mass (G). The lines for fawn carcass mass in northern (solid black line) and central Wisconsin (gray dashed line) in G appear superimposed because the slope and intercept for the 2 are nearly identical. Shaded areas are 95% confidence intervals



female carcass mass (partial R^2 ; Table 1). Similar to the fawn carcass mass model, cross-validation scores for the top model of female carcass mass indicated moderate fit and predictability ($R^2 = 0.29$, $MSE = 31.13$, $RMSE = 5.58$, $MAE = 4.38$). Adult female carcass mass increased with age from an expected average mass of 49.74 kg as yearlings to 56.13 kg by 15 years of age (Figure 3A). Adult female carcass mass also increased over the course of the hunting season from an expected average mass of 47.39 kg from 15 September (ordinal day 258) to 53.85 kg by 31 December (ordinal day 365; Figure 3B). Increasing percentage of oak forests within neighborhoods negatively affected female carcass mass across all regions, with expected average carcass mass decreasing from 52.62 kg to 46.30 kg as the percentage of oak forests increased from a minimum of 0% to maximum of 58% (Figure 3C). In central Wisconsin female carcass mass decreased from 52.37 kg to 43.01 kg as the percentage of hardwoods forests in their neighborhoods increased from a minimum of 2% to a maximum of 60%; however, no significant effect of the percentage of hardwoods in neighborhoods on female carcass mass was detected in southern or northern Wisconsin (Figure 3D).

For adult males, harvest date, age, and the percentage of row crops and pastures and grasslands within neighborhoods significantly affected carcass mass (partial R^2 ; Table 1). Region and WSI were in the top model but did not have a significant effects on male carcass mass. Cross-validation scores for the top model of male carcass mass were larger than those for fawns and females and indicated a better fit and predictability ($R^2 = 0.58$, $MSE = 70.16$, $RMSE = 8.38$, $MAE = 6.95$). Carcass mass of adult males increased nonlinearly with age, with younger deer gaining faster than older deer (Figure 4A). On average, the expected carcass mass of yearling males was 49.83 kg, whereas the expected mass of an 8-year-old male was 83.04 kg. During fall, carcass mass of adult males declined from an expected average mass of 88.39 kg on 15 September (ordinal day = 258) to 70.55 kg on 1 December (ordinal day = 335; Figure 4B). Expected average male carcass mass increased from 71.29 kg to 84.95 kg as the percentage of row crops in their neighborhoods increased from a minimum of 0% to a maximum of 68% (Figure 4C). Additionally, expected male carcass mass increased from 72.69 kg to 79.63 kg as the percentage of neighborhoods in pasture and grasses increased from a minimum of 0% to a maximum of 33% (Figure 4D).

Heart fat

The amount of heart fat fawns had accumulated in the fall differed by region, the percentages of pasture and grasslands, and available energy from woody browse (i.e., energy residuals from the woody browse index; Table 2). Goodness-of-fit tests indicated somewhat low predictive ability of the top fawn heart fat model (LR statistic = 5.0489, $P = 0.83$; $\chi^2_{114} = 118.14$, $P = 0.38$; deviance-squared = 91.04, $df = 114$, $P = 0.94$). Fawns in northern Wisconsin had a $93 \pm 7\%$ probability of having heavy heart fat, whereas fawns in central Wisconsin had a $51 \pm 17\%$ probability of having heavy heart fat and fawns in southern Wisconsin had a $15 \pm 7\%$ probability of having heavy heart fat (Figure 5A). Only fawns in southern Wisconsin had a $>1\%$ probability of having slight heart fat. The probability of fawns having heavy heart fat increased from $21 \pm 15\%$ to $91 \pm 10\%$ when the woody browse energy residual index for the forests in their neighborhoods increased (Figure 5B). Increasing percentages of pasture and grasslands also increased the probability of fawns having heavy heart fat from $28 \pm 8\%$ probability when there was no pasture and grasses available to $87 \pm 9\%$ probability when 30% of their neighborhoods were in pasture and grasses (Figure 5C).

Region, the start of green-up during the previous spring, and the previous winter WSI affected the probability of adult females having heavy, moderate, or slight heart fat during the fall (Table 2). Similar to fawn heart fat models, the goodness-of-fit tests indicated somewhat low predictive ability of the top adult female heart fat model (LR statistic = 16.331, $P = 0.06$; $\chi^2_{220} = 240.68$, $P = 0.16$; deviance-squared = 237.26, $df = 220$, $P = 0.20$). In southern and northern Wisconsin, the timing of spring green-up did not have a significant effect on adult female heart fat (Figure 6A, C). The probability of adult females having heavy heart fat in central Wisconsin declined $99 \pm 2\%$ when spring green-up started around 15 March (ordinal day = 74) to $14 \pm 7\%$ when spring green-up was delayed until

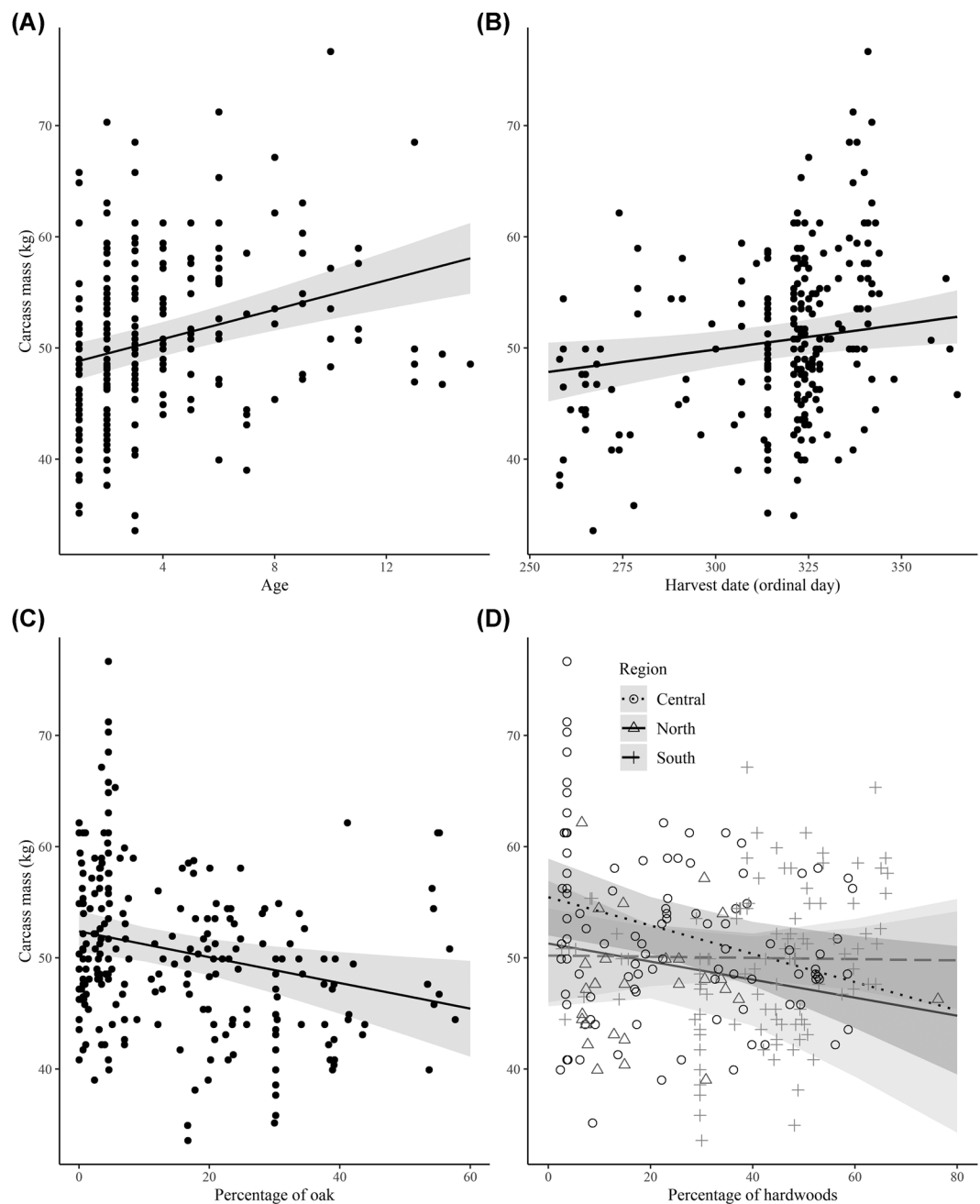


FIGURE 3 Effects plots for significant parameters in the top model of carcass mass for adult female white-tailed deer harvested in Wisconsin, USA, 2016–2018. Older females weighed more than younger females (A). Females harvested later in the hunting season weighed more than females harvested earlier in the hunting season (B). Among all regions, female carcass mass decreased as larger percentages of their neighborhoods were made up of oak (C). There was a regional interaction with hardwoods (D), where female carcass mass declined significantly as the percentage of hardwoods grew in central (dotted black line) Wisconsin, whereas no significant effect was detected in northern (solid gray line) or southern (long-dash gray line) Wisconsin. Shaded areas are 95% confidence intervals

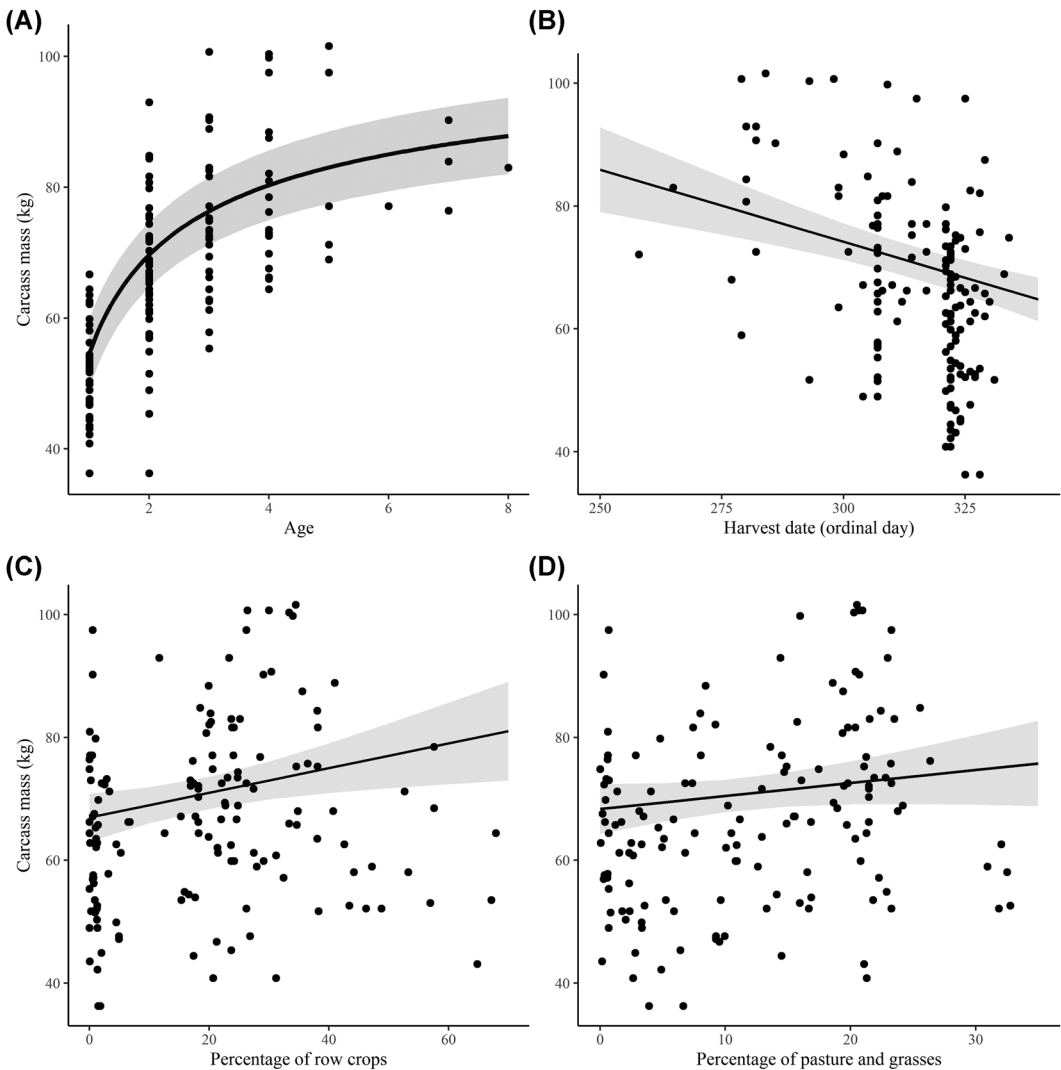


FIGURE 4 Fixed effects plots for significant parameters in the top model of carcass mass for adult male white-tailed deer harvested in Wisconsin, USA, 2016–2018. Older males weighed more than younger males, though younger males gained mass faster than older males (A). Males harvested later in the hunting season weighed less than males harvested earlier in the hunting season (B). Males also weighed more if their neighborhoods had a larger percentage of row crops (C) or pasture and grasses (D). Shaded areas are 95% confidence intervals

around 4 May (ordinal day = 124; Figure 6B). Regardless of region, as WSI of the previous winter increased from 0 to 60, the probability of adult females having heavy heart fat increased from about $17 \pm 9\%$ to $98 \pm 2\%$, whereas the probability of having moderate or slight heart fat declined from $54 \pm 6\%$ to $2 \pm 2\%$ and $29 \pm 13\%$ to $0 \pm 0\%$, respectively (Figure 6D).

Age, harvest date, and the energy available from woody browse affected the probability of adult male deer having heavy, moderate, or slight heart fat (Table 2). Similar to fawn and female heart fat models, the goodness-of-fit tests (Lipsitz test and Pulkstensis-Robinson chi-squared and deviance tests) indicated somewhat low predictive ability of the top adult male heart fat model (LR statistic = 11.727, $P = 0.23$; $\chi^2_{210} = 205.48$, $P = 0.58$; deviance-squared = 199.92, $df = 210$, $P = 0.68$). Regardless of age, the probability of adult male deer having heavy heart fat



TABLE 2 Coefficient values for independent variables in the top ordinal regression models of heart fat for white-tailed deer fawns, adult females, and adult males. Deer were harvested by hunters in Wisconsin, USA, 2016–2018. Est. = estimate, SE = standard error, Z = Z-value, P = P-value, WSI = winter severity index

Independent variables	Fawn heart fat				Female heart fat				Male heart fat			
	Est.	SE	Z	P	Est.	SE	Z	P	Est.	SE	Z	P
Harvest date	−0.02	0.29	−0.06	0.956	0.09	0.16	0.57	0.572	−0.10	0.22	−0.46	0.649
Age					0.10	0.16	0.65	0.515	−0.39	0.23	−1.68	0.094
Harvest date × age									0.55	0.28	2.00	0.046
Ecoregion Central	−2.55	1.24	−2.06	0.039	−0.32	0.73	−0.44	0.659				
Ecoregion South	−4.32	1.41	−3.06	0.002	−0.20	0.71	−0.28	0.780				
Ecoregion Central × start green-up					−1.72	0.51	−3.37	0.001				
Ecoregion South × start green-up					−0.42	0.29	−1.44	0.150				
Ecoregion North × start green-up					−1.22	0.71	−1.71	0.086				
WSI					0.93	0.31	3.04	0.002				
Pasture grass	1.08	0.45	2.38	0.017								
Energy scaled									0.55	0.27	2.03	0.042
Energy residual	0.68	0.33	2.09	0.037								

increased throughout Wisconsin with increasing energy availability from woody browse from $18 \pm 7\%$ to $69 \pm 29\%$ when other parameters were held at their means (Figure 7A). Among 1.5-year-old males, the probability of having heavy heart fat increased from $6 \pm 6\%$ to $37 \pm 12\%$ from 15 September (ordinal day = 258) to 1 December (ordinal day = 335; Figure 7B). The increase in heavy heart fat among 1.5-year-old males was the smallest increase among age classes. For example, among 2.5-year-old males the probability of having heavy heart fat increased throughout the hunting season from $1 \pm 3\%$ on 15 September (ordinal day = 258) to $50 \pm 20\%$ on 1 December (ordinal day = 335; Figure 7C). The probability of having heavy heart fat also increased throughout the hunting season for 3.5-year-old males from $1 \pm 1\%$ on 15 September (ordinal day = 258) to $63 \pm 27\%$ on 1 December (ordinal day = 335; Figure 7D). Among 4.5-year-old males the probability of having heavy heart fat increased from $1 \pm 1\%$ on 15 September (ordinal day = 258) to $75 \pm 28\%$ on 1 December (ordinal day = 335; Figure 7E).

Antler metrics

Region, age, the start of green-up, and the percentage of row crops affected the inside spread of adult male antlers (partial R^2 ; Table 3). Cross-validation scores for the top model of male antler inside spread indicated good fit and predictability ($R^2 = 0.72$, MSE = 35.41, RMSE = 5.95, MAE = 4.87). Inside spread increased nonlinearly with age and was dependent on region (Figure 8A). Inside spreads were wider in central and southern Wisconsin than inside spreads in northern Wisconsin. Regardless of region, the inside spread of average-aged adult male antlers decreased from an expected width of 35.39 cm when green-up started on 4 March (ordinal day = 63) to 28.87 cm if green-up started on 5 May (ordinal day = 125), an average decrease of 0.11 cm each day that the start of spring green-up was delayed (Figure 8B). There was no difference in decreasing antler spread among ages, with an average decrease of 0.10 cm observed per day of delayed green-up for 1.5-year-old males, and an average decrease of 0.11 cm

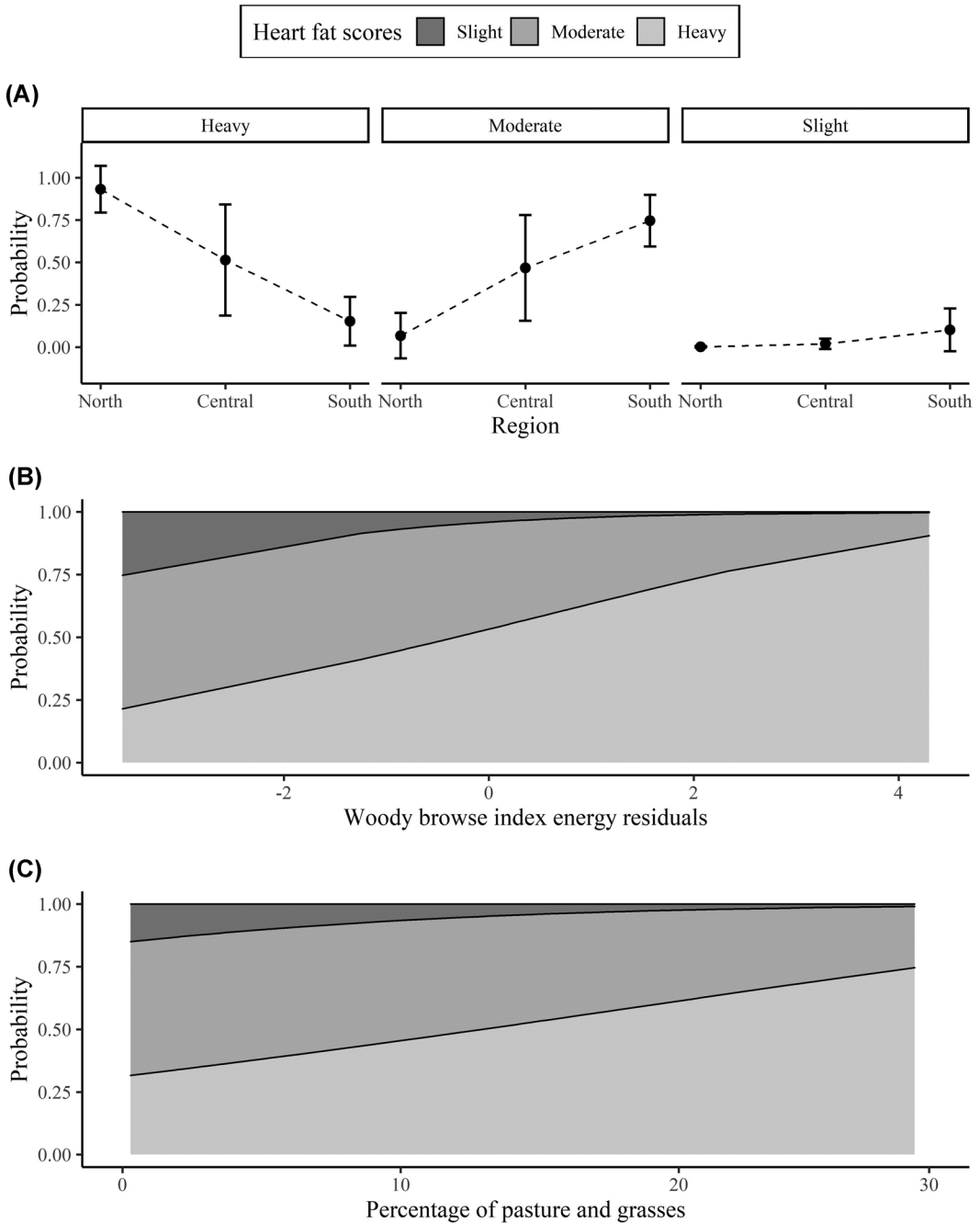


FIGURE 5 Fixed effects for significant parameters in the top model of heart fat for white-tailed deer fawns harvested in Wisconsin, USA, 2016–2018. The probability of having heavy heart fat was highest for fawns in northern Wisconsin and lowest for fawns in southern Wisconsin (A). Area plots indicate the change in the probability of fawns having heavy, moderate, or slight heart fat given the amount of energy available from woody browse (B) and the percentage of available pasture and grasses within neighborhoods (C). If energy per unit forested land was higher than expected (>0), fawns were more likely to have heavy heart fat and less likely to have moderate or slight heart fat in each ecoregion (B). The higher the percentage of pasture and grasses available in fawn neighborhoods, the higher the probability that fawns had heavy heart fat (C)

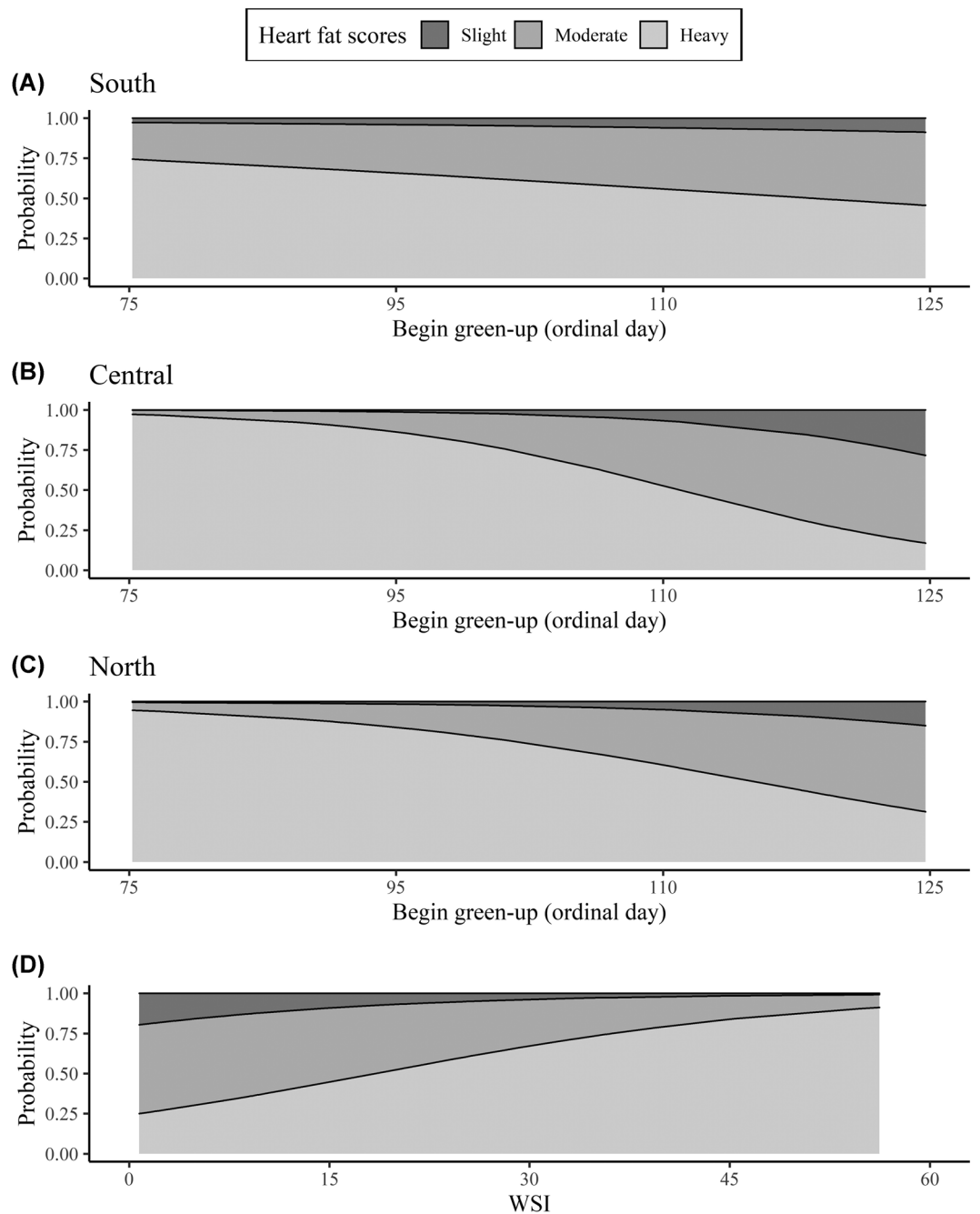


FIGURE 6 Fixed effects plot of significant parameters in the top model of heart fat for adult female white-tailed deer harvested in Wisconsin, USA, 2016–2018. Area plots indicate the change in probability of adult female deer having heavy, moderate, or slight heart fat given the date of spring green-up in southern (A), central (B), and northern Wisconsin (C). In northern and central Wisconsin adult females were less likely to have heavy heart fat and more likely to have moderate or slight heart fat when spring green-up was delayed, but the effect of spring green-up timing on female heart fat in southern Wisconsin was not significant. Adult females were more likely to have heavy heart fat when the winter severity index (WSI) of the previous winter was high (D), regardless of region

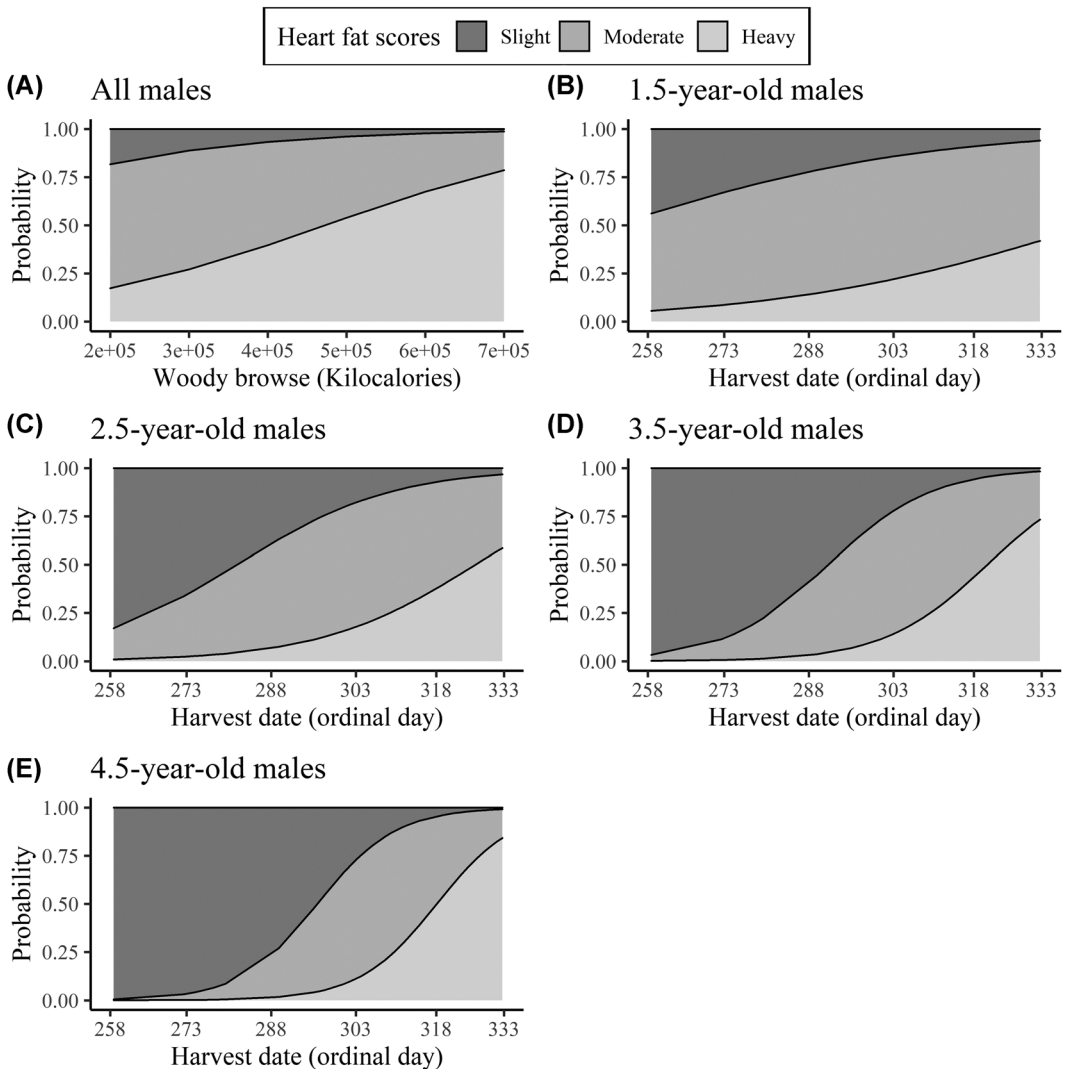


FIGURE 7 Fixed effects plots for parameters that had a significant impact on the probability of adult male white-tailed deer harvested in Wisconsin, USA, 2016–2018, having heavy, moderate, or slight heart fat. Area plots indicate the change in probability of male deer having heavy, moderate, or slight heart fat given the change in calories available from woody browse (A) and the date when males of different age classes were harvested (B–E)

observed per day of delayed green-up for 4.5-year-old males. The expected inside spread of average aged adult male antlers increased from 27.90 cm to 36.03 cm as the percentage of row crops within neighborhoods increased from 0% to 68% (Figure 8C), when the other parameters were held at their means.

Age and the percentage of conifer affected the basal circumference of main beams of adult male antlers (partial R^2 ; Table 3). Cross-validation scores for the top model of male antler basal circumference also indicated good fit and predictability ($R^2 = 0.62$, MSE = 2.19, RMSE = 1.48, MAE = 1.16). Basal circumference of main beams increased nonlinearly with age (Figure 9A). Basal circumferences decreased from an expected circumference of 9.7 cm to an expected circumference of 7.97 cm as the percentage of conifer available in neighborhoods increased from a minimum of 0% to a maximum of 34% (Figure 9B), when other parameters were held at the mean. This pattern was consistent among ages, with the basal circumferences of 1.5-year-old males decreasing from expected values of



TABLE 3 Coefficient values for independent variables in the top antler characteristic models of inside spread and basal circumference of the main beam for adult male white-tailed deer. Deer were harvested from across Wisconsin, USA, 2016–2018. Est. = estimate, SE = standard error, *t* = *t*-value, *P* = *P*-value, *p*. *R*² = partial *R*²

Independent variables	Inside spread (cm)					Basal circumference (cm)				
	Est.	SE	<i>t</i>	<i>P</i>	<i>p</i> . <i>R</i> ²	Est.	SE	<i>t</i>	<i>P</i>	<i>p</i> . <i>R</i> ²
Intercept	15.33	4.11	3.73	<0.001		9.37	0.22	43.24	<0.001	
Age ^{-0.5}	2.01	0.53	3.78	<0.001	0.12	-1.83	0.15	-12.41	<0.001	0.49
Start green-up	-0.13	0.06	-2.38	0.020	0.03					
Row crops	0.15	0.85	2.83	0.010	0.03					
Conifer						-0.36	0.18	-1.96	0.050	0.001
Aspen						-0.21	0.19	-1.96	0.27	0.000
Ecoregion Central	12.37	4.67	2.65	0.010	0.09					
Ecoregion South	11.70	4.73	2.47	0.020	0.07					
Ecoregion Central × age	-1.22	0.55	-2.22	0.030	0.04					
Ecoregion South × age	-1.15	0.55	-2.09	0.040	0.04					

6.85 cm to 6 cm and the basal circumferences of 4.5-year-old males decreasing from expected values of 11.50 cm to 10.55 cm as the percentage of conifer in neighborhoods declined.

DISCUSSION

Our results indicate that the timing of spring green-up has an important effect on deer body condition in fall even following mild winters, which suggests spring green-up is an independent influence of deer condition when winters are not severe. Our results also suggest that when spring green-up begins is more important than the length of the green-up period. A later spring green-up date had negative effects across age and sex classes of deer in our study, whereas the length of the green-up period had no effect on deer condition. The negative effects of delayed spring green-up manifested in different body condition response variables for each age and sex class. Fawns had less mass, adult females had less heart fat, and adult males had smaller antlers when spring green-up occurred later in the year. These results are similar to other studies of northern ungulates where earlier spring green-up indices correlated with heavier animals (Myserud et al. 2001), and higher reproductive rates (Sæther 1985). The expected effect of early green-up, and thus early access to nutritional vegetation is a positive effect on deer body condition (Pettorelli et al. 2006, Simard et al. 2014), which our results support. Simard et al. (2014), however, reported the opposite pattern; they reported that delayed, rapid green-up in spring was correlated with better body condition in the fall. In their study, Simard et al. (2014) attribute better deer body condition following a delayed spring green-up to a more rapid green-up that led to overall higher quality vegetation throughout the summer.

Winters during our 3-year study were considered mild throughout Wisconsin. During these mild winters we did not observe an effect of WSI on fall body condition of adult male deer but did observe an influence on the body condition of fawns and adult females, albeit the opposite of what was predicted. Fall fawn carcass mass and adult female heart fat were positively correlated with the WSI of the winter prior to harvest. Severe winters can have marked effects on northern ungulate populations directly through winter die-offs due to starvation and indirectly

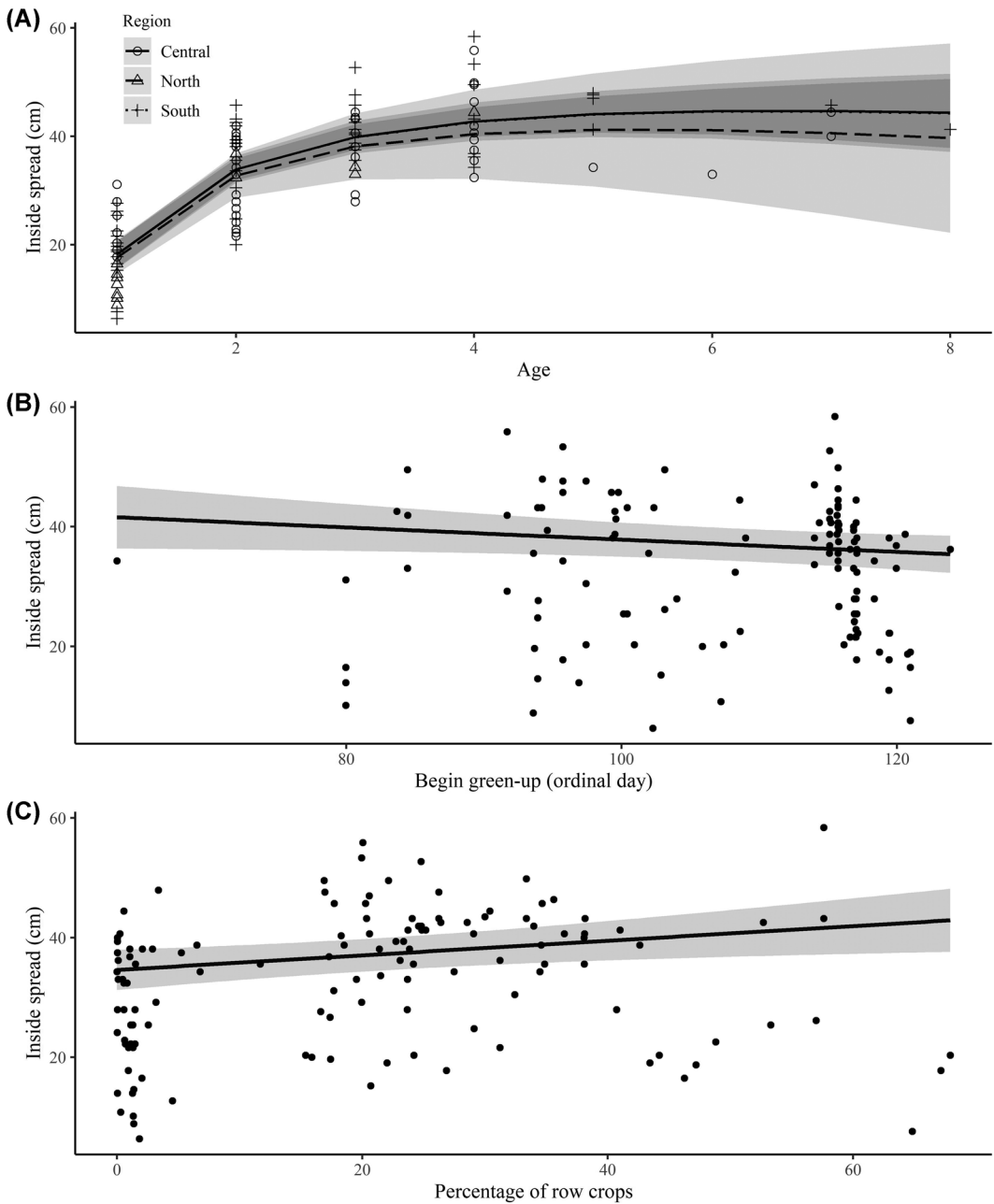


FIGURE 8 Fixed effect plots for significant parameters in the top model of inside antler spread for adult male white-tailed deer harvested in Wisconsin, USA, 2016–2018. Inside spread increased nonlinearly with age and was dependent on region (A). The long-dashed line represents inside spread of males in northern Wisconsin, the dotted line represents those in central Wisconsin, and the solid line represents those in southern Wisconsin. The lines for inside spread in southern (solid gray line) and central Wisconsin (dotted black line) in A appear superimposed because the slope and intercept for the 2 are nearly identical. Later spring green-up resulted in smaller inside spreads in the fall among ages (B). Inside spread of antlers increased with increasing percentages of row crops in neighborhoods among all ages (C). Shaded areas are 95% confidence intervals

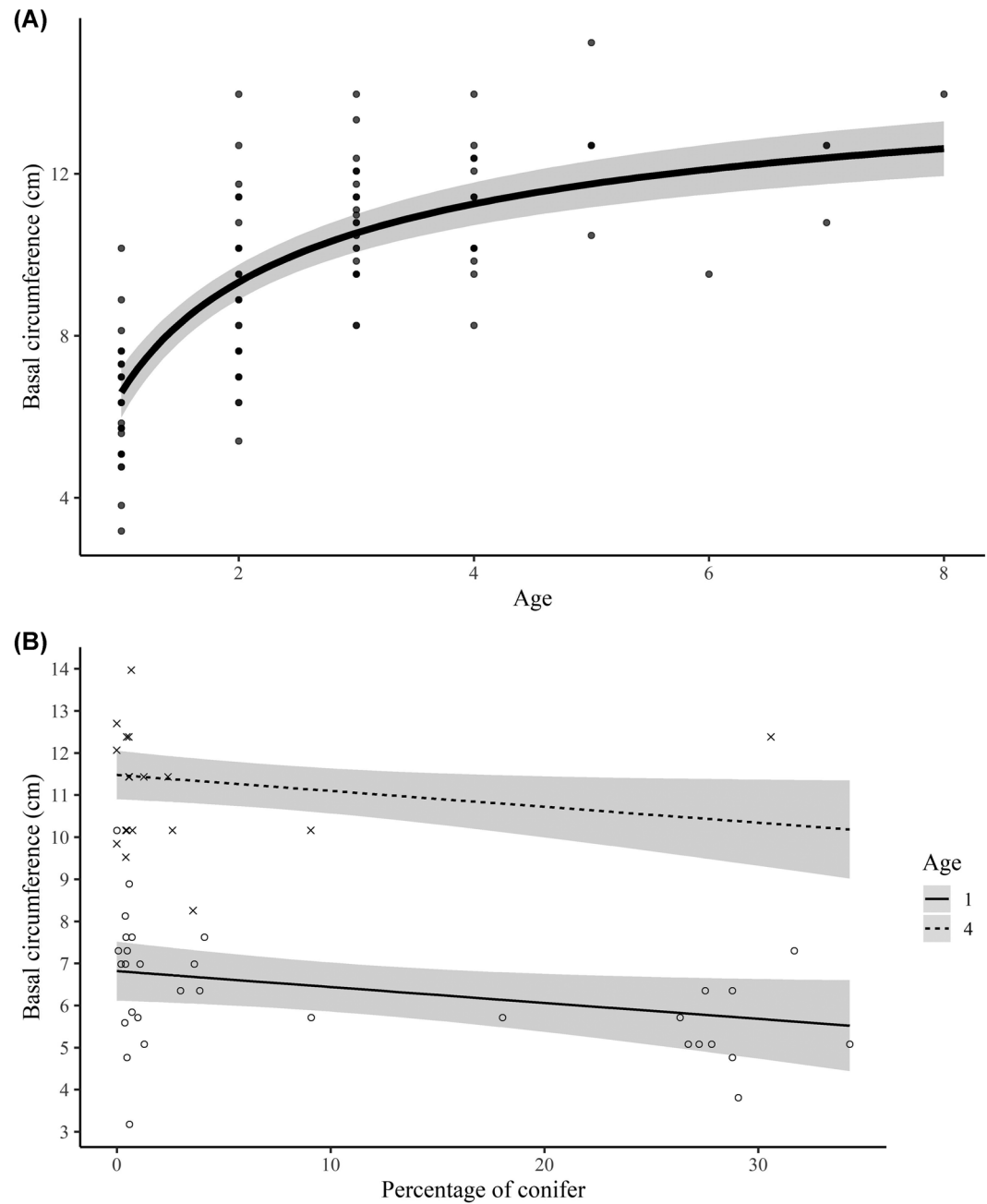


FIGURE 9 Fixed effect plots for significant parameters in the top model for basal circumference of antlers of adult male white-tailed deer harvested in Wisconsin, USA, 2016–2018. The basal circumference of antlers increased nonlinearly with age (A). Basal circumference of antlers decreased with increasing percentage of conifer in neighborhoods among all ages (B). Predicted values for ages 1.5 and 4.5 years are plotted along with points for both age groups. Open circles represent 1.5-year-old males and × represent 4.5-year-old males. Shaded areas are 95% confidence intervals



through increased efficiency of predators. Direct effects of severe winters can persist into the following growing season, manifesting as smaller body masses and lower pregnancy rates (Loison and Langvatn 1998, Parker et al. 2009, Duquette et al. 2014). In mild winters, however, such as those that occurred during our study, malnutrition among individuals was minor and the effects were often not observed at the population level (Whitlaw et al. 1998, Patterson and Power 2002).

We suggest that the positive relationship observed between the previous winter's severity with heart fat of adult females and carcass mass fawns may be a spurious result. Only 4 of 795 deer in our study experienced a moderate winter by our index; all other deer experienced mild winters. The limited range of WSI values during our study were not typical of conditions that would induce malnutrition in most deer (DelGiudice 1998 and DelGiudice et al. 2006) and likely would not have carry-over effects on body condition in the subsequent fall. Our results, in concert with other studies (DelGiudice et al. 2002, Patterson and Power 2002) with more severe winters, suggest a nonlinear relationship between winter severity and deer health and population demographics.

The WSI we used was a point-based system where -17°C is valued the same as -34°C and 45 cm of snow is valued the same as 100 cm of snow on any given day throughout winter. From 1960 through 2017 in northern Wisconsin, the average annual WSI value has been 60.8 ± 4.2 and there have been 14 winters that were considered severe or very severe, only 1 of which has occurred since 2000 (i.e., 2013–2014). Without any of our data including the severe or very severe WSI category, it is uncertain if our results would have changed and showed WSI to be more predictive of population health during those conditions. Our results do show that WSI provides limited information about deer condition following mild winters.

In the more heavily forested northern and central regions of Wisconsin, fawn carcass mass increased with increasing percentage of oak forests while in the more agriculturally dominated southern region of Wisconsin, access to oak forests had no effect on fawn carcass mass. Fawn survival and pregnancy rates, which are directly related to body condition, were also positively related to the abundance of agricultural lands or habitat with high nutritional planes in Wisconsin (McCaffery et al. 1998), Illinois (Nixon et al. 1991, Green et al. 2017), and Pennsylvania (Vreeland et al. 2004). While our study measured the percentage of oak forest available to fawns and there was a positive relationship between oak availability and fawn mass, other researchers reported that fawn mass and survival rates were positively related to fall use of oak forests specifically during good mast years (Feldhamer et al. 1989, Wentworth et al. 1992, McShea and Schwede 1993). We were unable to measure mast abundance in our study but recognize that mast production is highly spatially and temporally variable (Healy et al. 1999, Greenberg 2000, Pérez-Ramos et al. 2014), which could have contributed to regional differences in effect that we observed.

We also speculate that the high nutritional plane afforded fawns with access to agricultural lands in southern Wisconsin may have masked the benefits associated with availability of oak forests, while in more heavily forested northern and central Wisconsin where agriculture is generally scarce, access to oak forests as a food source is more beneficial regardless of the level of mast production in a single year. Summer deer diets in agriculturally dominated landscapes can be composed predominately of crop forage (Nixon et al. 1991, Daigle et al. 2004), while summer deer diet in heavily forested regions can consist of up to 68% woody browse (Kohn and Mooty 1971). Regardless of region, fawns with access to pasture or grasslands and forests with larger amounts of biomass from woody browse had the highest probabilities of having heavy heart fat. We attribute this result to forests providing a year-round source of browse. Grasslands do play a key role in fawn habitat as they are the first cover type to green-up in the spring, providing an important nutrient source when deer condition is at its most vulnerable. While croplands provide a nutrient-rich habitat, in Wisconsin, most row crops do not emerge until June and crops tend to be harvested by late fall. For these reasons the combination of forests and grasslands provide a more reliable year-round food source.

Fawns in northern Wisconsin had a higher probability of having heavy heart fat than fawns in central and southern Wisconsin, when controlling for other habitat characteristics. Fawns in northern regions that experience severe winters trade-off body growth for higher fat reserves, likely as an adaptation for winter survival because surviving the first winter is critical in the lifespan of northern deer (Lesage et al. 2001). This trade-off could explain



why we observed heavier fawns in southern Wisconsin but higher probabilities of heavy heart fat in fawns in northern Wisconsin. Fawns in southern Wisconsin experience milder winters and have access to highly nutritious agricultural landscapes, which allows for higher rates of growth and lower overwinter energy storage requirements, whereas fawns in northern Wisconsin typically experience more severe winters and have higher energy requirements, during which time they rely on energy reserves for survival.

Adult female carcass mass was negatively affected by the amount of hardwood forests and oak forests within their neighborhoods, with no regional interactions. Oak forests are typically considered high quality habitats in Wisconsin because oak is a preferred browse species (Castleberry et al. 1999, Wakeland and Swihart 2009) and acorns are an important seasonal food source for deer (Pekins and Mautz 1987). We expected that given the high forage value of oak forests in terms of browse and mast, females with higher percentage of oak forests in their neighborhoods would have larger masses than those with lower percentages of oak forests. One potential explanation for oak forests having a negative effect on adult female body condition but a positive effect on fawn body condition could be that over-browsed oak forests result in lower forage availability during the spring and summer but provide ample forage in fall in the form of fallen acorns. Fawns may respond more quickly to the increased availability of high-quality mast because fall represents a greater proportion of their life to that point than it does for adult females.

An alternative explanation in the context of fawns benefiting from increased access to oak forests, is that adult females may have more success at rearing fawns when they have access to higher quality habitats such as oak forests in fall, and that the energetic investment of successfully raising fawns results in reduced mass gain compared to barren females (Therrien et al. 2007). The energy requirement of lactation for white-tailed deer with 2 fawns is approximately 4 times higher than basal rates (Moen 1978), and >95% of pregnant adult female deer in the Midwest have twins annually (Green et al. 2017). Without the added energy requirements of lactation, nonlactating females gain significantly more fat than lactating females (Cothran et al. 1987). Lactating females gained 30 g less/day than non-lactating females in Quebec, Canada (Therrien et al. 2007). As is the case with most data from harvested deer, we were unable to track individuals over time, and therefore were unable to determine if adult females successfully raised fawns and what the associated effects on body condition could have been. Most fawns are born in late May and are weaned by September (i.e., at 80 days old; Gauthier and Barrette 1985, Therrien et al. 2008) in northern latitudes and the majority of deer are harvested in November, which would make determining the number of females lactating or not during the hunting season an underestimate of the true rate of fawn survival.

Adult female heart fat was not affected by habitat composition, woody biomass, or the quality of woody biomass within neighborhoods. This suggests weather conditions have a stronger effect on fat accumulation than our habitat measures and that longer growing seasons allow for sufficient accumulation of fat regardless of habitat composition for adult female deer. Organ fat accumulates before subcutaneous fat and is mobilized after subcutaneous fat (Mautz 1978), making it less responsive to within-season variation in habitat quality and behavior when subcutaneous fat is present. We speculate that regional onset of spring green-up had a significant effect on female heart fat by influencing the length of the growing season and thus increasing access to more nutritious spring and summer forage available in many habitats. These conditions have lasting effects across seasons and are likely to be reflected in fat deposits where fat is stored longer.

Adult males had greater mass when there was a larger percentage of agricultural lands within their neighborhoods. This was the case across Wisconsin, with no regional effects despite the large differences in habitat composition among regions. Access to forests with an abundance of woody browse led to a higher probability of males having heavy heart fat. This supports the concept that different environmental conditions contribute to different physiological demands (Parker et al. 2009). Specifically, our results for male deer also support evidence of the order in which fat is accumulated and mobilized (Mautz 1978). Woody browse is a relatively consistent presence in forested portions of deer neighborhoods despite seasonal fluctuations in biomass and nutritional value, while the availability of crop forage is highly seasonal, with associated large fluctuations in abundance due to annual cycle of planting and harvest. If carcass mass is an integrator of subcutaneous fat, then we expect carcass mass to



be more of a reflection of highly seasonal forage such as crops. Heart and other organ fat are accumulated before subcutaneous fat, likely reflecting forage availability and quality from an earlier period during the growing season. Because of the order in which fat is accumulated and metabolized, heart and other organ fat appear to be less reliable indicators of deer health when subcutaneous fat is present.

Percentage of agricultural lands positively influenced the inside spread of antlers in adult male deer, whereas percentage of coniferous forests negatively affected the basal circumferences of main beams. Our results support the evidence provided by Strickland and Demarais (2008) in Mississippi, USA, that land use types that encourage growth of early successional herbaceous plants, including row crop and pasture or grassland, positively influence antler size of deer. Additionally, in Georgia, USA, habitat composition with larger percentages of agricultural lands favored larger antlers, while larger percentages of conifer forests in most regions were associated with smaller antler size (Quebedeaux et al. 2019). Conifer forests typically have lower quantity and quality browse components than other forest cover types used by deer (Verme 1965). Adult male deer may also use agricultural lands in avoidance of females in the summer, which could increase their reliance on crops as forage and contribute to the positive relationship between antler size and available agriculture (Nixon et al. 1991). Cain et al. (2019) reported that high-contrast edges (i.e., field-forest edges), heterogeneous land cover, and high variation in soil productivity were associated with more large-antlered deer harvested in an examination of Boone and Crockett records across the midwestern United States. We did not include soils in our study; however, soil and land cover types are highly correlated in Wisconsin (Kotar 1986, Fasnacht and Gower 1998).

Surprisingly few studies have examined the spatially explicit environmental factors contributing to antler size of white-tailed deer (Kissel et al. 2002, Strickland and Demarais 2008, Jones et al. 2010, Heffelfinger 2018, Cain et al. 2019). Our results add to this growing body of literature and are in agreement with the evidence provided in these studies that nutrition is a limiting factor affecting antler size, and that conifer forests are not conducive to large antler size.

We faced numerous challenges in our effort to study deer condition, which limits the inferences we can make. In many instances, our models had relatively modest amounts of explained variance, which is a consequence of several factors. The amount of variation in morphometric variables that can possibly be explained using environmental covariates is inherently limited because much of the observed variation is due to maternal or genetic factors (Monteith et al. 2009, Michel et al. 2016, Jamieson et al. 2020). This is not unique to our study, and indeed, our study explained similar amounts of variation as other studies that examined environmental influences, but not maternal or genetic factors, of white-tailed deer morphometrics (Jones et al. 2010, Simard et al. 2014, Quebedeaux et al. 2019). Additionally, assessing environmental covariates based on harvest locations imperfectly measures the environment to which each deer was exposed, which was why we buffered harvest locations to twice the area of an average deer home range in Wisconsin. Other challenges we faced during our study were a lack of variation in a key covariate, the winter severity index, and some of our models had relatively small sample sizes because we relied on samples from hunter-harvested deer. Yet despite those limitations, we did reveal a consistent effect of spring green-up on fall deer condition, which is a relatively novel result in much of North America, where winters receive the most attention. That we found this result, despite our study limitations suggests the robustness of spring green-up as a phenomenon that influences deer populations and spring green-up is worthy of further study.

One aspect of our data collection that deserves extra scrutiny is our use of citizen scientists. Cost and personnel constraints and statewide coverage precluded collecting data using agency staff, but citizen scientists made this possible. While we considered our partnerships with Wisconsin hunters successful, such an approach is not without drawbacks. Citizen scientists are more likely than professional biologists to make data collection errors that result in data loss (0–30% depending on the response metric, in our case); thus, some amount of data loss should be expected when using citizen science volunteers (Crall et al. 2011). The higher levels of data loss, in our case, were due to a combination of errors in data collection, damage to hearts sustained by shooting, and inability of the lab we employed to assign ages to some teeth. A portion of these errors and loss of data are to be expected regardless of whether trained professionals or trained citizen scientists collect data. Loss of data for metrics like



carcass mass and antler dimensions ranged from 0–7%. Finally, our sample sizes and geographic coverage was determined by the number and location of willing volunteers, thus was not fully within our control.

We maintained high levels of hunter participation and follow-through by implementing simple protocols and incentivizing hunters by providing an (ostensibly accurate) cementum-annuli age for each deer and annual project reports. Hunters could complete data collection in about 10 minutes/deer. To offset the potential consequences of not using professional biologists to collect data, we provided clear guidance and training opportunities, and asked for measurements of body condition that were easy to collect, were familiar metrics often recorded by hunters for their own records, and were well rooted in the literature as indicators of deer health. Data submitted by hunters suggests that large-scale monitoring of deer health can be accomplished with citizen participation and using simple indices that can easily be measured with minimal training. Protocols used in this study could be adapted for large-scale population health and demographics research and monitoring efforts for a variety of ungulate species.

MANAGEMENT IMPLICATIONS

Population-level effects of severe winters on northern deer herds is well documented; however, the role of spring green-up timing in influencing deer populations has largely been unappreciated. We documented that spring green-up is an independent driver of deer body condition with lasting, measurable effects. Managers interested in weather effects on deer herd health should consider measures of spring green-up timing in conjunction with traditional measures of winter severity.

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CONFLICT OF INTERESTS

The authors acknowledge that there are no conflicts of interest to report for this study.

ETHICS STATEMENT

All deer used in our study were legally harvested under the state of Wisconsin hunting laws and regulations.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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