



Scale-dependent habitat selection is shaped by landscape context in dispersing white-tailed deer

Ryan B. Stephens · Joshua J. Millspaugh · Jon T. McRoberts ·
David R. Heit · Kevyn H. Wiskirchen · Jason A. Summers ·
Jason L. Isabelle · Remington J. Moll

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Abstract

Context Identifying how animals select habitat while navigating landscapes is important for understanding behavioral ecology and guiding management and conservation decisions. However, habitat selection may be spatially and temporally plastic, making it challenging to quantify how species use resources across space and time.

Objectives We investigated how landscape context and dispersal shape habitat selection at multiple spatial scales in white-tailed deer (*Odocoileus virginianus*).

Methods Using step-selection functions, we quantified habitat selection of landcover and topographic covariates at three spatial scales for juvenile males during three movement periods (before, during, after dispersal) in two regions of Missouri, USA—a

fragmented, low forest cover region with rolling hills, and a forested, topographically variable region.

Results Although selection for forest cover increased after dispersal in both regions, deer selected forest cover at smaller spatial scales in the fragmented, low forest cover region. This result indicates scale of selection was dependent on forest availability and configuration with deer likely perceiving landscapes differently across their distribution. Functional responses to topography differed in magnitude and direction between regions with deer avoiding roads and selecting valleys in the rolling hills region (especially during dispersal) while showing no response to roads and selecting for ridgelines (during dispersal) in the topographically variable region. This result suggests movement behavior is strongly dependent on topography.

Conclusions Although deer may select similar habitats among regions, landscape context and movement period shape the scale, strength, and direction of

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R. B. Stephens (✉)
Department of Biological Sciences, East Tennessee State
University, Johnson City, TN 37614, USA
e-mail: stephensrb@etsu.edu

R. B. Stephens · D. R. Heit · R. J. Moll
Department of Natural Resources and the Environment,
University of New Hampshire, Durham, NH 03824, USA

J. J. Millspaugh · J. T. McRoberts
Wildlife Biology Program, University of Montana,
Missoula, MT 59812, USA

J. J. Millspaugh
Department of Environmental and Forest Biology, College
of Environmental Science and Forestry, State University
of New York, Syracuse, NY 13210, USA

K. H. Wiskirchen · J. L. Isabelle
Missouri Department of Conservation, 3500 East Gans
Road, Columbia, MO 65201, USA

J. A. Summers
Missouri Department of Conservation, 2901 W Truman
Blvd, Jefferson City, MO 65109, USA

selection. This result has important implications for how animals use landscapes across different regional contexts.

Keywords Movement ecology · Resource selection · Spatial scale · Step-selection function analysis

Introduction

Habitat selection is a key behavioral process that shapes the movement of species within and across landscapes (Millsbaugh and Marzluff 2001; Manly et al. 2002). Understanding this process is critical for guiding landscape-level management and conservation practices, particularly in the context of habitat preservation, gene flow, and disease transmission (Slarkin 1985; Cullingham et al. 2011; Walter et al. 2011; Holbrook et al. 2017). However, habitat selection and movement dynamics are often spatially and temporally plastic and depend upon the broader landscape context, particularly the availability and configuration of habitat (Levin 1992; Morales and Ellner 2002; Schick et al. 2008). For instance, animals often demonstrate a functional response of increasing selection as available habitat decreases, a pattern that is driven by broader regional patterns of landcover mosaics (Godvik et al. 2009; Roever et al. 2012). Additionally, the spatial configuration of landscape features can influence habitat selection depending on composition and level of fragmentation (Stubblefield et al. 2006; Radford and Bennett 2007). These patterns can further vary temporally as both resources and abiotic conditions change throughout the year (Holbrook et al. 2017). Collectively, these spatial and temporal factors underscore the need to assess habitat selection in a framework that is likewise spatially and temporally dynamic.

Habitat composition and configuration also can influence how animals perceive landscapes, which in turn can change the spatial scale at which individuals respond to a given habitat characteristic (Laforge et al. 2016). An individual's perceptual range within a landscape partly defines the scale at which it responds to the environment, and such perceptions vary according to habitat type and topography (Olden et al. 2004). For example, prey species may perceive and respond to the landscape at smaller spatial scales

in habitats with denser vegetation compared to more open areas where predator vigilance requires them to perceive the landscape at larger spatial scales (Jayakody et al. 2008; Laforge et al. 2016). Thus, when evaluating habitat selection it is important to consider the scale of effect for a given habitat covariate (Laforge et al. 2016; Heit et al. 2023).

The type of movement an animal exhibits may further modulate habitat selection and the scale of that selection (Killeen et al. 2014; McGarigal et al. 2016). Two of the most common movement types in motile animals are home range ("station-keeping") and dispersal movements (Burt 1943; Schlägel et al. 2020). These movement types have distinct characteristics, with dispersal movements typically being faster and straighter than those in home ranges (Soulsbury et al. 2011; Moll et al. 2021). During dispersal, terrestrial animals often select habitat features that provide greater cover while allowing for ease of movement (Long et al. 2005; Cox and Kesler 2012). In more topographically complex areas, valleys are often used during dispersal since they are relatively easy to transverse (Puskas et al. 2010). Movement type may also change an individual's perception of the landscape and in turn the scale at which it selects habitat (Lima and Zollner 1996; Nathan et al. 2008). For example, spatial memory within home ranges may allow individuals to select habitat at finer scales compared to dispersing or migrating individuals that may use landscape cues to select habitat at larger scales (Fagan et al. 2013).

We quantified how landscape context and dispersal shape seasonal habitat selection, and the spatial scale of that selection in a widespread and highly mobile ungulate, the white-tailed deer (*Odocoileus virginianus*; hereafter deer). Although both sexes and all demographic classes of deer may disperse (e.g., Nixon et al. 2007; Anderson et al. 2015; Lutz et al. 2015; Moll et al. 2021), juvenile males (~10–20 months of age) make up the greatest proportion of dispersing individuals (Long et al. 2008). Deer dispersals tend to be relatively brief and directional, but vary both seasonally and by landscape context (Long et al. 2010). For example, most juveniles disperse in the spring or fall, with spring dispersal driven by inbreeding avoidance (facilitated by adult female aggression) and fall dispersal by mate competition with adult males (Long et al. 2008). These seasonal dispersals often differ in length with longer dispersals in the spring relative

to fall (Long et al. 2008). All dispersals differ from within-home range movements, which are typically slower, less directional, and centered on one or more core areas where food and cover is plentiful (Moll et al. 2021). Forest cover is one of the most important habitat variables affecting both within-home range (Heit et al. 2023) and dispersal movements in deer, with higher rates of dispersal and distance traveled in areas with less forest cover (Nixon et al. 2007; Diefenbach et al. 2008; Lutz et al. 2015). Additionally, during dispersal, topographic features such as rivers and roads act as semipermeable barriers that influence dispersal movements (Long et al. 2010; Moll et al. 2021). Although dispersal has been well studied in deer, it is unclear how habitat selection during dispersal compares to that of within-home range movements (but see Gilbertson et al. 2022; Hooven et al. 2023) and how spatial scale and landscape heterogeneity interact to modulate habitat selection.

We analyzed habitat selection and movement attributes of male juvenile deer in two study areas in Missouri, USA during three different periods—before, during, and after dispersal (Fig. 1a, b). We took advantage of natural variation in both landcover and topography between the two study areas to examine how landscape context shapes habitat selection. One study area was in an agricultural region with rolling hills and low forest cover, and the other in a forested region with considerable topographic variation (Fig. 1). We used step-selection functions to quantify habitat selection using high-resolution data from three landscape cover variables (forest, forest edge, cropland; Fig. 1c–e) and three topographic variables (topographic position index, distance to water, and distance to roads; Fig. 1f–h) at three spatial scales. We hypothesized that the strength and scale of habitat selection would be dependent on movement period and would vary between seasons and by study area (Table 1). Specifically, we predicted that during a dispersal, deer would select resources at larger spatial scales since they would have less spatial memory, or familiarity with their surroundings (Fagan et al. 2013). Additionally, we predicted that during dispersal, deer would show stronger selection for landcover variables that provide cover (e.g., forest, forest edge) and topographical features that help facilitate and direct movement (e.g., valleys and water ways) than either before or after dispersal and that areas with greater mortality risk (i.e., roads) would be

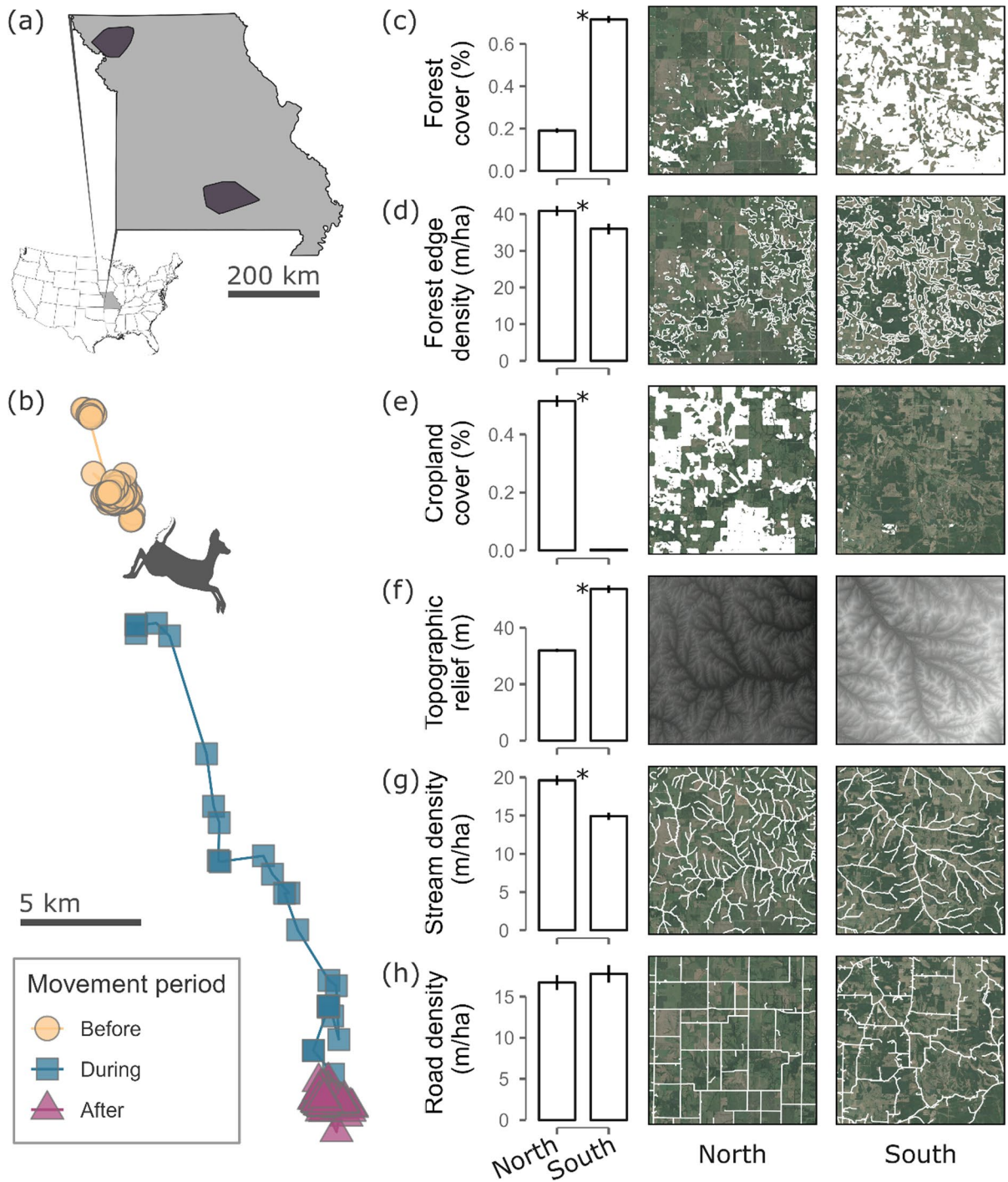
avoided (Table 1). We also predicted that agriculture would be avoided in the spring, when it provides little cover, compared to the fall when agricultural crops provide both cover and food (Gilbertson et al. 2022). However, during late spring, agriculture can provide substantial forage in this study area, so an alternative prediction was that selection for agriculture would be positive across seasons. Lastly, we expected faster and more direct movements during dispersal compared to home range movements (Killeen et al. 2014; Moll et al. 2021).

Methods

Study system

Our study took place in the northwestern and south-central portions of Missouri (hereafter North and South, respectively), which are over 300 km apart and differ considerably in both landcover and topographical features (Fig. 1a, c–h). Landcover in the North consisted of highly fragmented forest patches (19% of landscape) in a mosaic of grasslands (26%) and cultivated croplands (51%) (Fig. 1c–e). Comparatively, landcover in the South consisted of more contiguous forest (72%) with interspersed grassland patches (26%) and almost no cropland (<1%) (Fig. 1c–e). The fragmented nature of forest patches in the North resulted in a higher forest edge density (Fig. 1d). Forests in both study areas were primarily composed of oak (*Quercus* spp.) and hickory (*Carya* spp.) with the South also having smaller amounts shortleaf pine (*Pinus echinata*) (Wright et al. 2019). Grasslands were used for cattle grazing or hay production in both study areas and corn and soybeans were the primary row crops in the North (Wright et al. 2019).

Topography in the North was characterized by rolling hills whereas the South (in the Ozark Highlands region) had steep hills and valleys with nearly twice the local relief (Fig. 1f). Streams and waterways were abundant in both regions with the North having slightly higher stream density than the South (Fig. 1g). Although road density was similar between study areas, flatter areas in the North accommodated a gridded road system whereas the hillier areas in the South had a more variable road layout that generally followed the terrain (Fig. 1h).



Both study areas had deer hunting seasons during fall with an archery season extending from mid-September through mid-January and a primary firearms season in mid-November. Additionally, there was an antlerless-only firearm season in early

December, youth firearm seasons in late October and late November, and an alternative methods season in late December/early January. Hunting pressure is high with over 500,000 permit holders in the

◀**Fig. 1** Locations **a** of the two study areas (North and South) in Missouri, USA, **b** example of a white-tailed deer (N17014) with locations before, during, and after a spring dispersal, and **c–e** landcover and **f–h** topographic characteristics for each study area shown as mean values ($\pm 95\%$ confidence intervals) and square satellite view insets (10×10 km near center of study area). Values for means were extracted from 1000 random locations (1 km^2 area) within each study area and compared with t -tests. Within insets, habitat characteristics are shown in white except for topographic relief which is elevation (low = black, high = white). Forest, forest edge, cropland, topographic relief, and stream density differed between study areas (asterisks denotes $\alpha < 0.05$), whereas road density was similar ($P = 0.135$). The amount of grassland was similar ($t = 0.01$, $P = 0.99$) between the North (25.8%) and South (25.7%) but was not included in habitat selection models due to multicollinearity with other variables (see *Habitat selection analysis* in Methods). Deer silhouette by Gabriela Palomo-Munoz (<https://creativecommons.org/licenses/by-nc/3.0/>)

state and around 300,000 deer harvested annually (Keller et al. 2017).

Deer collaring and dispersals

Deer were captured using modified Clover traps or rocket nets between January and March of 2015–2019 and were chemically immobilized for collaring (see Wright et al. 2019 for details). Each individual was assigned a unique deer ID number and fitted with an Iridium global positioning system (GPS) radio-collar (model G2110E, 825 g; Advanced Telemetry Systems, Isanti, Minnesota, USA) that recorded locations every 5 h. During handling, deer were aged based on tooth eruption and wear patterns as follows: fawn (6 months), yearling (1.5 yr), and adult (> 1.5 yr) (Severinghaus 1949). All trapping and immobilization protocols were approved by the University of Missouri Institutional Animal Care and Use Committee (protocol number 8216).

To avoid differences in habitat selection and movement that may vary among sexes and demographic groups, our analyses included only juvenile males (i.e., fawns at capture and those dispersing between ~ 10 – 20 months of age) which comprise the majority of dispersing deer within a population (Gilbertson et al. 2022). We defined a dispersal as a permanent emigration from one home range to a new range, such that ranges do not overlap (Diefenbach et al. 2008; Haus et al. 2019). We visually screened deer locations to identify individuals with multiple location clusters, signifying a potential dispersal

event using QGIS (v. 3.28.1; QGIS Development Team 2022). We defined a ‘dispersal window’ as the time period between when individuals exited a cluster of locations and established to another cluster.

Dispersal events in deer generally take place in either spring or fall, with proximate causes of dispersal, along with habitat quality, differing between seasons (Long et al. 2008). Applying season designations similar to Gilbertson et al. (2022), we classified dispersal events as occurring during spring (April 1–July 31) or fall (September 1–December 31). Within a season, we modeled home ranges before and after dispersal using kernel density estimation (95% adaptive kernel, reference bandwidth) in R (R Core Team 2021) with default setting in the *amt* package (Signer et al. 2019). For home range estimates we excluded points that fell within a two-day buffer on either side of the dispersal window to avoid atypical movements that could occur either before a dispersal or when initiating a new home range following a dispersal. We used points that fell within the home range polygon for modeling habitat selection before and after a dispersal. We only retained deer that had at least 50 points within a home range (Seaman et al. 1999). Using a one-day buffer on either side of the dispersal window, we identified locations associated with dispersal as points that fell between the last point within the pre-dispersal home range and the first point within the post-dispersal home range. This allowed us to exclude points associated with exploratory movements which occasionally occurred before a dispersal. Some dispersals took place in a short timeframe; we only modeled habitat selection during the dispersal period for deer that had at least nine locations (i.e., dispersing for at least 45 h), which we considered the minimum acceptable sample size for step-selection analysis (see below). For seven individuals, dispersals took place over a longer period where they moved repeatedly back and forth between the two home ranges. For these deer we did not analyze any locations associated with the dispersal but did analyze their before and after dispersal locations to compare habitat selection in pre- and post-dispersal home ranges.

Habitat selection covariates

We collected landscape covariates that we hypothesized could shape habitat selection or movement

Table 1 Habitat selection covariates for white-tailed deer and their predicted selection coefficient (positive [+], none [~], negative [–]) within home ranges (HR) and during dispersal (Disp.)

Covariate	Description and data source	Prediction		Hypothesis/reason
		HR	Disp.	
Forest	Proportion forested land cover from Dynamic World LULC (Brown et al. 2022)	+	+	HR: Cover and food (Beier and McCullough 1990); Disp.: Cover for movement (Gilbertson et al. 2022)
Agriculture	Proportion agricultural land cover from Dynamic World LULC (Brown et al. 2022)	+	–	HR: Important food source in fall (Kie et al. 1991). Disp.: Provides little cover for movement, especially in spring (Gilbertson et al. 2022)
Grassland	Proportion grassland from Dynamic World LULC (Brown et al. 2022)	+	+	HR & Disp.: Provides bedding and forage, particularly in spring (Gould and Jenkins 1993; Grovenburg et al. 2011)
Forest edge	Edge density calculated from Dynamic World LULC ((Brown et al. 2022)	+	+	HR & Disp.: Provides foraging opportunities and cover (Williamson and Hirth 1985)
Topographic position index	Average TPI based on DEM (USGS 2022a)—valleys (negative values), flats or continuous slopes (values near zero), and ridges or hills (positive values)	~	–	HR: Important in mountainous regions (strongly related to forage), but likely less important in non-mountainous areas (Volk et al. 2007). Disp.: Flats or valleys facilitate movement, especially in hilly areas (Dussault et al. 2007; Puskas et al. 2010)
Distance to water	Average distance to water based on streams (flowlines), rivers, and waterbodies in the National Hydrography Dataset (USGS 2022b)	~	–	HR: Although important in arid areas (Carson and Peek 1987), likely less important in humid areas. Disp.: Important for direct- ing dispersal movements (Long et al. 2010; Clements et al. 2011; Gilbertson et al. 2022)
Distance to roads	Average distance to road based on U.S. Census TIGER county-level road shapefiles (U.S. Census Bureau 2019)	–	–	HR & Disp.: Avoided due to potential mortality (Long et al. 2010; Kämmerle et al. 2017)

Predictions represent hypotheses based on theory and/or are supported by previous studies

of deer (Table 1) including four variables related to landscape cover (forest, forest edge, cropland, and grassland; Fig. 1c–e) and three related to topography and linear features (topographic position index, distance to water, and distance to roads; Fig. 1f–h). We characterized landscape cover using Dynamic World land use land cover (LULC) classifications, which are based on machine learning of 10 m Sentinel-2 imagery (Brown et al. 2022). We used Google Earth Engine (Gorelick et al. 2017) to generate a composite Dynamic World LULC at a 10 m pixel resolution based on imagery between June 1, 2015 (earliest imagery available) through Dec. 31, 2019 (end of study period), taking dominant LULC for each pixel. From the Dynamic World LULC we used ‘trees’ to represent forest, ‘crops’ to represent cropland, and ‘grass’ to represent grassland. We calculated forest edge density (m/ha) using ‘forest’ relative to other landcover types (with ‘built’ LULC classification removed) with the function ‘lsm_l_ed’ in the *landscapemetrics* R package (version 1.5.6; Hesselbarth et al. 2019). To quantify topographic position, we used a Digital Elevation Model (DEM; 10 m pixel resolution) from the United States Geological Survey National Elevation Dataset (USGS, 2022a) to create a topographic position index (TPI) in QGIS. Pixel values were based on a neighborhood radius of 5 cells with negative values indicating valleys, values near zero indicating flats or continuous slopes, and positive values indicating ridges or hills. To represent water, we used the high-resolution shapefiles of streams (flowlines), rivers, and waterbodies in the National Hydrography Dataset (scale of 1:24,000, USGS 2022b) to build a raster (10 m pixel resolution) with cells representing distance to nearest water feature. For roads, we used both paved and unpaved roads from the U.S. Census TIGER county-level road shapefiles (U.S. Census Bureau 2019) to generate a distance to nearest road raster (10 m pixel resolution).

Habitat selection analysis

We determined habitat selection using a step-selection function analysis which compares observed steps (pairs of consecutive GPS points) to available steps. We generated available steps associated with an observed GPS location as the start point of the step and a random end point based on changes in distance moved (step length) and bearing (turning

angle) (Thurfjell et al. 2014). For each observed step of an individual deer during each movement period (before, during, or after dispersal), we generated nine available steps by fitting a gamma distribution to the observed step lengths and the von Mises distribution to the turn angles using the ‘amt’ R package (Thurfjell et al. 2014; Signer et al. 2019). Because deer respond to landscape features at different spatial scales (Heit et al. 2023), we used observed and available locations (end point in step) to extract each landscape cover covariate (as a proportion; forest edge as a density) and topographic covariate (as mean cell values) at three spatial scales (30 m, 90 m, and 270 m radii) using the *raster* R package (version 3.5.21; Hijmans 2022).

We evaluated habitat selection among movement periods by fitting step-selection functions as generalized linear mixed models (GLMMs) using the ‘glmmTMB’ function in the *glmmTMB* R package (version 1.1.5; Brooks et al. 2017). Following Muff et al. (2020), we included step-specific fixed intercepts along with deer-specific random slopes for each movement (step length and turning angle) and habitat covariate to account for individual variation in habitat selection. Before fitting full models, we first determined the appropriate spatial scale for each habitat covariate within a study area and movement period by fitting models that contained movement covariates and a single habitat covariate at each of the three spatial scales and selected the scale with the lowest Akaike Information Criterion (AIC) score (the scale of effect). When models with different scales had delta AIC values < 2 , we used the smaller spatial scale which often has the greatest functional response (Laforge et al. 2016). We then checked for collinearity ($r > 0.6$) among habitat covariates. In the South, forest and grassland were highly correlated ($r = 0.95$), and in the North, forest, grassland, and cropland were not highly correlated ($r < 0.55$) but had high variance inflation factors (≥ 3). Consequently, we removed grassland from models in both study areas which reduced all correlations and variance inflation factors to acceptable levels (Zuur et al. 2010; Dormann et al. 2013). Due to cropland being absent in the South, we separately fit final GLMMs for both study areas. Models included each three-way interaction between season (spring, fall), movement period (before, during, and after dispersal), and a habitat covariate or movement parameter. We centered and

scaled all continuous covariates prior to analysis. In all models, we included natural log of step length and cosine of turning angle to reduce bias in the parameter estimates (Forester et al. 2009). Within a season and habitat covariate, we also tested for differences among movement periods with post hoc comparisons using estimated marginal means and Bonferroni corrections in the *emmeans* R package (version 1.7.5, Lenth 2018). Additionally, to more fully assess effect sizes of significant variables in the GLMMs, we plotted relative selection strength following Avgar et al. (2017) and used a smoothed function (a generalized additive model with $k=3$) fit to model-predicted selection at available points to visualize changes in selection across the value range for each covariate.

Movement analysis

To more fully understand how movement parameters changed before, during, and after a dispersal, we further assessed changes in turning angle and speed. We used the *amt* R package to extract turning angle, distance, and time for each step. We compared turning angles among movement periods using analysis of variance for circular data by applying the function ‘aov.circular’ in the *circular* R package (version 0.4.95; Agostinelli and Lund 2022). We calculated speed (m/h) by dividing step length by elapsed time and compared it among movement periods within a study area and season using linear mixed effects models in the ‘lme4’ R package (version 1.1.30; Bates et al. 2015) followed by post hoc comparisons with estimated marginal means and Bonferroni corrections using the *emmeans* R package. We included deer ID and year as random effects for this analysis.

All statistical analyses were performed in R version 4.0.4 (R Core Team 2021). Variance around

means is presented as ± 1 SE unless otherwise noted. We considered variables significant at $\alpha < 0.05$. Additionally, given relatively small sample sizes for dispersal locations (see Results), and less power to detect differences, we also highlight trends ($0.05 < \alpha < 0.1$) for dispersals.

Results

Across the five-year study period, 104 out of 622 collared deer dispersed, including 7.9% of juvenile females (6 of 76), 0.6% of adult females (1 of 178), 41.7% of juvenile males (80 of 192), and 6.6% of adult males (17 of 259) (note that some individuals lived multiple years and therefore the sum of demographic bins exceeds the number of total deer). For juvenile males, three exhibited both distinct spring and fall dispersal events and these individuals were subsequently used for both spring and fall dispersal analyses. We acknowledge these as exceptions to the traditional definition of dispersals, but these movements were clearly not migratory in nature and thus we considered them unique, dispersal-like movements. For juvenile males, observations were distributed (number of deer [GPS locations] for the spring and fall, respectively) in the North before (22 [6,550]; 22 [4,464]), during (8 [221]; 11 [219]), and after (22 [6,454]; 23 [11,247]) a dispersal and in the South before (6 [1,662]; 29 [5,816]), during (4 [88]; 9 [380]), and after (7 [1,842]; 28 [10,856]) a dispersal (Table 2). For juvenile males, dispersal metrics were similar on average between study areas with distances ranging from 1.1 to 52.1 km and taking between < 5 h to 15 days to complete (Table 2). On average, spring dispersals took place in late May and early June and fall dispersals took place in mid-October (Table 2).

Table 2 Summary of number of 1.5-yr-old white-tailed deer and associated GPS locations by movement period relative to the timing of dispersal events used in habitat selection models along with dispersal movement parameters for each study area and season

Study area	Season	Deer (GPS locations)			Dispersal movement parameters					
		Movement period			Distance (km)		Duration (days)		Start date (month/day)	
		Before	During	After	Mean (SE)	Range	Mean (SE)	Range	Mean (SE)	Range
North	Spring	22(6,550)	8(221)	22(6,454)	9.4(1.5)	2.1–27.7	2.7(0.8)	< 5 h–15.0	6/2(2.9)	5/4–7/9
	Fall	22(4,464)	11(219)	23(11,247)	5.3(1.1)	1.1–20.9	2.8(0.7)	< 5 h–13.3	10/18(3.0)	9/12–11/9
South	Spring	6(1,662)	4(88)	7(1,842)	10.9(4.1)	4.0–30.4	3.7(1.4)	20 h–10.4	5/26(10.7)	4/4–6/7
	Fall	29(5,816)	9(380)	28(10,856)	8.4(2.2)	1.3–52.1	3.3(0.8)	< 5 h–12.7	10/20(3.0)	9/11–11/12

Habitat selection

Sample size of deer (4 to 29) and GPS locations (88 to over 10,000) varied among seasons, movement periods, and study areas (Table 2).

The scale of effect for habitat covariates (as determined by univariate models) differed both among movement periods and among study areas (Fig. 2). In particular, deer in the South tended to select habitat covariates at larger spatial scales than deer in the North, especially for forest, forest edge, and topographic position index (Fig. 2).

Selection patterns for landscape cover variables were similar between study areas, whereas selection patterns for topographic features varied between the two study areas (Fig. 3, Fig. 4; full model results including all parameter estimates and *P*-values are in Supporting Information, Table S1). We note that relatively small sample sizes during the spring season in the South may have limited our ability to detect differences (Table 2). In both study areas, and across seasons and movement periods, deer selected forest and forest edge, and tended to increase selection for forest after a dispersal, whereas selection for edge decreased in the spring and stayed consistent (North) or increased (South) in the fall. In the North, cropland generally had little effect on habitat selection regardless of season or movement period. Despite less topographic relief in the North, deer selected for valleys (negative values) across movement periods and showed particularly strong selection for valleys

during dispersal (Fig. 4). Comparatively, in the South, deer selection for valleys before a dispersal but selected for ridges (positive values) during dispersal, particularly in the fall. In the North, deer selected for areas farther away from water before a dispersal and areas closer to water after a dispersal in the spring, and in the South, deer selected areas closer to water before a dispersal in the fall. Additionally, during fall dispersals, deer in both study areas showed a trend of selection for areas closer to water. In the North, deer selected areas farther from roads both during and after dispersal events, whereas deer in the South showed little selection toward roads except before a dispersal in the spring.

Movement

Turning angles differed among movement periods in both study areas and seasons with movements during dispersals having turning angles centered on 0 (indicating straight-line movements) whereas before and after dispersal movements tended to be more evenly distributed with slight peaks closer to 180°, indicating back-tracking movements (Fig. 1b, Fig. 5a). Speed also varied by movement period, but patterns differed between spring and fall (Fig. 5b). In the spring, deer moved over twice as fast during a dispersal compared to either before or after the dispersal. Although deer moved faster during a dispersal in the fall, movements after a dispersal were significantly faster than before a dispersal.

Fig. 2 Best scale (radius) for habitat covariates in each study area as determined by AIC. Filled shapes indicate significant ($\alpha < 0.05$) habitat selection within a habitat covariate and movement period in at least one season within GLMMs (see Fig. 3). Note that during a dispersal there were several scales within 2 Δ AIC for some habitat covariates; although these are indicated in the figure, the smallest scale was used in models

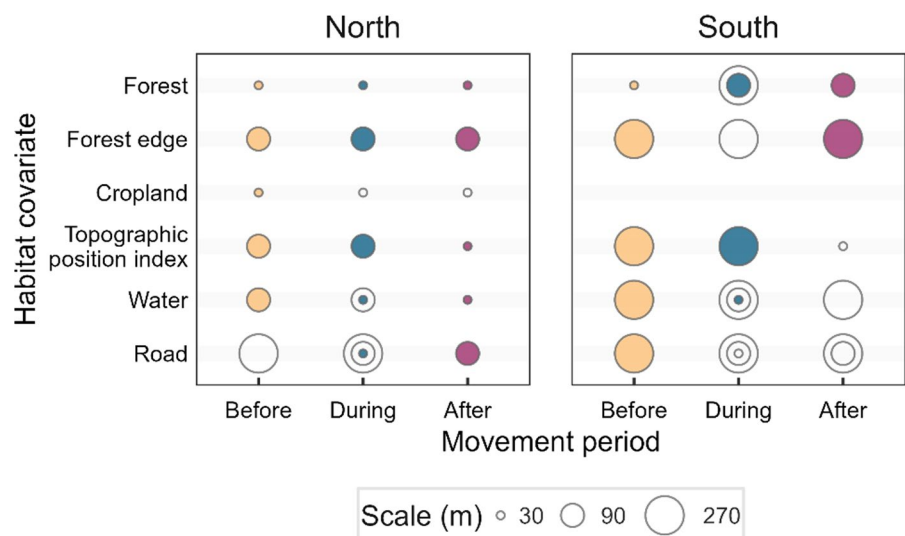
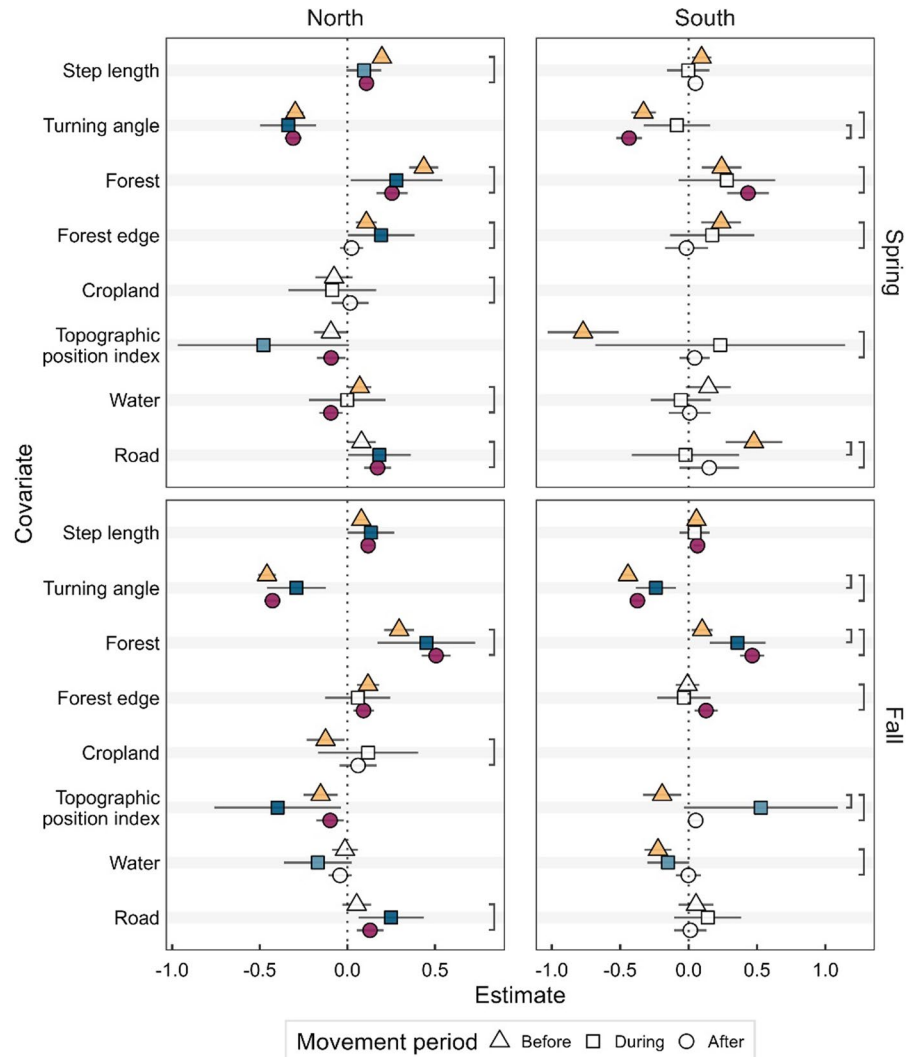


Fig. 3 Results of GLMMs for the North and South study areas (Missouri, USA) indicating movement responses (step length and turning angle) and habitat selection (all other covariates) during dispersal movement periods and between seasons. Shapes are coefficient estimates and lines are 95% confidence intervals. Filled shapes indicate significant ($\alpha < 0.05$) movement responses and habitat selection within a movement period. Additionally, trends ($0.05 < \alpha < 0.10$) are indicated with a light blue for dispersals. Within a study area, season, and covariate, movement periods connected by vertical brackets are significantly different as indicated by post hoc tests with Bonferroni correction (full model results are in Supporting Information, Table S1)



Discussion

We observed similar habitat selection patterns for landcover variables (related to forest cover and configuration) between study areas, but the spatial scale at which forest was selected depended on availability and landscape configuration. Comparatively, selection for topographical features (topographic position index, waterways, roads), and the strength of that selection, differed by study area and movement period. Overall, season had a relatively small influence on habitat selection but did influence speed of movements. Together, these results suggest that although deer selected similar habitat covariates between our two study areas, the scale, strength,

and direction of selection was shaped by both landscape context and movement period. This finding has important implications for how deer use the landscape in different regions which can ultimately influence population-level processes such as disease transmission and gene flow patterns.

Habitat selection and scale

Deer consistently selected for forest across movement periods and seasons. Forests provide food (browse and mast) and cover during movement and rest periods (Beier and McCullough 1990; Stewart et al. 2011; Gilbertson et al. 2022). Although we did not detect stronger selection for forest during dispersal

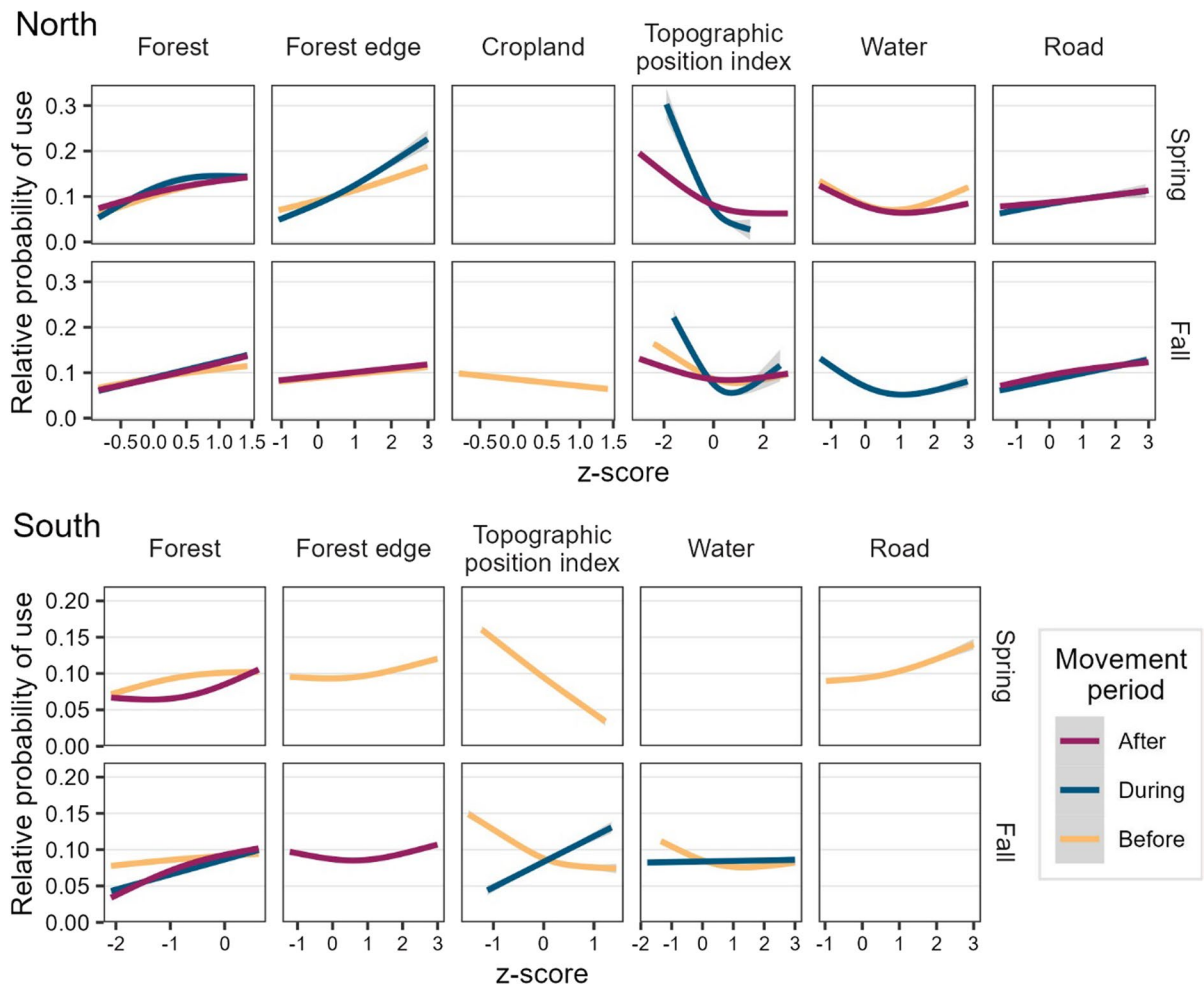


Fig. 4 Relative selection strength for habitat covariates in the North (top) and South (bottom). Only significant covariates from GLMMs within a movement period are shown. Lines are

smoothed functions (generalized additive models with $k=3$) fit to model-predicted selection at available points

compared to home range movements, deer tended to select more forest cover after a dispersal compared to before. This result suggests that deer are actively seeking forested post-natal home ranges that provide forage and cover. Although the effect size and direction of selection for forest appeared to be similar between study areas, we found that the spatial scale of this selection differed (Figs. 2, 3, 4). In the North, where forest was relatively scarce, we observed selection at smaller spatial scales compared to the South where forest was more abundant. This difference in scale of effect may relate to both availability and configuration, where the North had less forest and was fragmented, often composed of narrow tracts (Fig. 1c,

d) causing deer to select forest at smaller spatial scales as they track forest cover. We also found that the scale at which deer selected forest was smaller than the scale at which they selected forest edge. This difference in apparent perception may be due to more predator vigilance at forest edges (Jayakody et al. 2008), which often have higher densities of mesopredators such as coyotes (Kays et al. 2008). Overall, the spatial scale of effect for landcover variables was generally small (i.e., 30 m radius). This scale is considerably smaller than many studies use for deer and was only possible given the high-resolution, 10-m landcover data available with Dynamic World LULC (Brown et al. 2022). Future studies of habitat

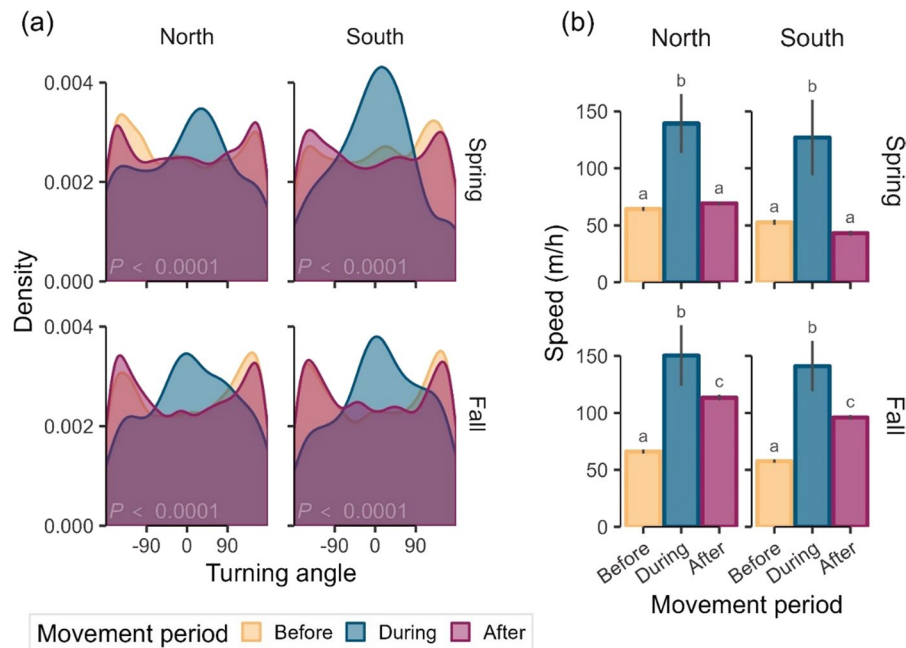


Fig. 5 Differences in **a** distribution of turning angles and **b** mean movement speed ($\pm 95\%$ confidence intervals) among movement periods (before, during, and after a dispersal event) and between study areas and seasons. Inset P -values from analysis of variance for circular data indicate significant differences in mean direction of movements among movement periods. For movement speed, within a study area and season,

movement periods with the same letters are not significantly different, whereas movement periods with different letters are significantly different as indicated by linear mixed effects models and post-hoc tests with P -values adjusted with Bonferroni correction (full model results are in Supporting Information, Table S2)

selection in deer, and other large mammals, may benefit from analyzing a variety of scales, including smaller spatial scales than have traditionally been considered.

Topographic features such as rivers and valleys can help direct movement in dispersing animals and can bound the home range of some individuals during day-to-day movements (Long et al. 2010; Clements et al. 2011; Gilbertson et al. 2022). We found that deer in both study areas selected areas closer to streams and rivers but only consistently during fall dispersal. Waterways may provide a relatively easy pathway to follow and the thicker vegetation, often found along riparian areas, may provide cover during the fall hunting season when deer seek additional concealment (Lone et al. 2015). Compared to other topographic and linear features, topographic position index had the strongest effect on habitat selection during dispersal movements, although patterns differed between the two study areas (Figs. 3 and 4). In the rolling hills of the North, deer selected valleys,

whereas in the more topographically variable South, deer selected ridgelines. These differences may be attributed to landscape context and how deer perceive their environment. In the North, it is unlikely that the rolling hills impede movement compared to other regions where more rugged terrain with steep slopes necessitate ungulates to use valleys for movement corridors (Dussault et al. 2007; Killeen et al. 2014). However, given limited forest cover in the North study area, deer may use other features for cover such as valleys (or depressions in the landscape) that help reduce visibility as they move through open areas. Indeed, visual assessments of dispersal points in the North revealed that deer often selected low areas while moving through agricultural fields and grasslands. In addition to potential foraging opportunities, this may also explain why we did not see strong selection against agriculture in the spring. Valleys were also important during home range movements, but the magnitude of selection was considerably less than during the dispersal period.

Interestingly, although deer in the South selected valleys during home range movements, they selected ridgelines during dispersal, contrary to our expectations. The high percent of forest cover in the South likely had sufficient cover for concealment during dispersal events and home range activities. Therefore using ridgelines for dispersal may help reduce energy expenditure (compared to using steeper slopes; e.g., Killeen et al. 2014), while providing a large viewshed of the surrounding area to select the movement path (Olden et al. 2004). In agreement with this interpretation, we also found that during dispersal, deer in the South selected topographic position index at a larger scale than in the north (Fig. 2). This result suggests that deer are perceiving the landscape at larger extents, which may be facilitated by more expansive viewsheds along ridgelines. In both study areas the confidence intervals around selection for topographic position index during dispersal were large, which is likely a consequence of limited sample size coupled with individualistic habitat selection (Hooven et al. 2023).

We predicted that deer would avoid roads during both home range and dispersal movements. However, we found differential responses to roads between the study areas with deer in the agricultural North avoiding roads (particularly during and after dispersal) and deer in the more forested South showing little selection toward roads. Peterson et al. (2017) found similar results in Wisconsin where deer in an agricultural region were less likely to cross roads compared to deer in a forested region. Although deer are generally thought to avoid roads due to higher risk of mortality from vehicular collisions (Long et al. 2010), it appears that landscape context plays an important role in structuring this selection. In our study, road density was similar between the two study areas, but configuration differed dramatically (Fig. 1h). This configuration may be important as roads in the North generally followed a grided system making them easier to predict whereas roads in the South generally followed the topography of the landscape (e.g., ridgelines), making them less predictable and potentially occurring along paths that deer were selecting for during dispersal. Alternatively, roads that intersect forest may not be perceived as an obstacle compared to roads that pass through more open areas.

Movement

We expected that dispersal movements would be faster and more directional than movements within home ranges. Indeed, we found that deer tended to move on more directed paths and moved about twice as fast during a dispersal compared to within home ranges either before or after a dispersal. This pattern has previously been found in a variety of birds and mammals (Delgado et al. 2009; Soulsbury et al. 2011; Killeen et al. 2014), including white-tailed deer (Moll et al. 2021). Theoretical models indicate that moving in a straight-line search is more efficient at finding open territories (Zollner and Lima 1999), and thus may be the most energetically efficient way to disperse when selecting a new home range. Comparatively, spatial memory within the home range, as deer use resources, generates shorter non-directional movements (Van Moorter et al. 2009). Additionally, the faster movements that we observed during dispersal may reduce contact with conspecifics when moving through the home ranges of other individuals (Killeen et al. 2014). During home range movements, we found that speed was similar before and after a dispersal in the spring, but was faster following a dispersal in the fall. This increased speed in the fall may be because juvenile males are searching for mating opportunities (Schultz and Johnson 1992). Alternatively, food limitations later in the season may also increase speed as individuals move more across the landscape to find resources.

Conclusion

Dispersal is a key life history event which has received considerable theoretical and empirical study in terms of variation in habitat selection before and after dispersal events (Stamps et al. 2005; Day et al. 2019). Although there has recently been more effort devoted toward understanding how animals select and move through their environment during dispersal (e.g., Killeen et al. 2014; O'Neill et al. 2020; Frankish et al. 2022; Thorsen et al. 2022; Orgeret et al. 2023), there are still large knowledge gaps, even for well-studied species such as white-tailed deer. Our study found nuanced ways in which deer alter habitat selection and movement during dispersal; in particular showing stronger selection for waterways and

topographical features. These results are in line with deer dispersing in Wisconsin that selected for areas near rivers and also another ungulate (elk; *Cervus elaphus*) which demonstrated a different selection response to topography during dispersal (Killeen et al. 2014; Gilbertson et al. 2022). However, habitat selection during dispersal is likely highly species specific with avian and terrestrial carnivores often showing less responsiveness to environmental gradients during dispersal movements (O'Neill et al. 2020; Thorsen et al. 2022; Orgeret et al. 2023). Such differences in how animals move through the landscape has potential implications for how animals perceive the landscape during this life history event. A better understanding of habitat selection during dispersal can help inform landscape connectivity planning (e.g., managing specifically for habitat selected during dispersal) and has implications for broad-scale landscape connectivity in the face functional fragmentation due to anthropogenic development and climate change.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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