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Research article

Seasonal fine-scale resource selection of elk in the central Appalachian Mountains

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Resource selection by animals varies depending on spatial and temporal context, thus it is important to account for these factors when conducting studies that examine this behavior relative to the availability and distribution of resources. Many resource selection studies combine fine-scale animal location data obtained using global positioning system (GPS) technology and coarse-scale, remotely sensed, spatial layers. Fewer studies combine fine-scale animal location data with vegetation data collected in the field, which can identify important fine-scale drivers of resource selection. Understanding fine-scale resource selection of ungulates inhabiting regions dominated by closed-canopy forests may provide important information regarding management actions that improve habitat quality. From April 2021 to August 2022, we conducted vegetation surveys at locations (n = 1294) used by 39 GPS-collared elk *Cervus canadensis* and at paired random locations (n = 2509) available to elk. We used conditional logistic regressions to compare seasonal (spring, summer, fall, winter) vegetation characteristics between used and available locations. We also conducted a species indicator analysis to compare plant species found at used and available locations during peak foraging periods (dawn/dusk). Regardless of season, the probability of use by elk increased as tree basal area (m^2/ha) decreased, and the presence of herbaceous plants increased. Clovers (*Trifolium* spp.) were indicators of locations used by elk during primary foraging periods regardless of season. Other plants that were indicators of locations used by elk during at least one season included purple-crown vetch *Securigera varia*, bird's foot trefoil *Lotus corniculatus*, and black medick *Medicago lupulina*. This research highlights the importance of managed openings, ecotones, and other communities characterized by reduced tree cover and increased herbaceous plants to meet the foraging needs of elk in landscapes dominated by closed-canopy forests. Creating and maintaining managed herbaceous openings and restoring open-forest communities will likely facilitate elk population growth and expansion.

Keywords: *Cervus canadensis*, conditional logistic regression, elk, fine-scale, GPS, habitat management, resource selection

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Introduction

The interplay between species behavior and the availability of resources at different temporal and spatial scales are known to influence patterns of movement and resource selection (Johnson 1980, Arthur et al. 1996, Boyce and McDonald 1999). Therefore, the evaluation of resource selection across multiple scales is important, particularly when the goal is to inform management (Johnson 1980, Manly 2002, Roberts et al. 2017). While multiscale studies that use resource selection functions (RSFs) are not uncommon (McGarigal et al. 2016, Linden et al. 2018), they typically rely solely on GPS tracking technology coupled with remotely sensed data such as National Land Cover Data (NLCD) (Anderson et al. 2005a, Hebblewhite and Haydon 2010). In the early years of using GPS technology, location accuracy was low (Tomkiewicz et al. 2010), justifying the use of remotely sensed environmental data to provide information at a coarse spatial scale (i.e. cover type at 30 × 30 m resolution). Current GPS technology has increased accuracy, with location error ranging from 8 to 15 m (Smith et al. 2021). As such, using coarse-scale remotely sensed environmental data along with highly accurate GPS animal location data can limit the ability to assess fine-scale resource selection. Moreover, remotely sensed data layers do not capture all environmental features, such as plant biomass and species composition, that are known to influence resource selection behaviors (Fleming et al. 2004, Briand et al. 2009). Resource selection studies that incorporate fine-scale data, while logistically challenging, can more effectively capitalize on highly accurate GPS-telemetry data to better understand the factors influencing animal movements and resource selection (Lamont et al. 2019, Hooven et al. 2024).

Because of their significant ecological, economic, and cultural importance, ungulates including elk *Cervus canadensis* (Anderson et al. 2005b), moose *Alces alces* (Brown et al. 2018), caribou *Rangifer tarandus* (Briand et al. 2009), bison *Bison bison* (DeMars et al. 2020), and white-tailed deer *Odocoileus virginianus* (Jenkins et al. 2007) have long been the focus of resource selection studies. Such studies have examined diverse topics like predator avoidance (Hebblewhite and Merrill 2009, McGreer et al. 2015), seasonal foraging behavior (Jenkins et al. 2007, Thompson et al. 2015), parturition (McLaren et al. 2017), and response to human disturbances (Brown et al. 2018, DeMars et al. 2020). While past research has substantially improved our understanding of ungulate resource selection at landscape scales, studies that incorporate detailed environmental and ecological data collected on the ground to understand fine-scale selection patterns are less common (Briand et al. 2009, McGreer et al. 2015). Nonetheless, there is a growing acknowledgement of the need for studies that incorporate fine-scale environmental data to further characterize ungulate resource selection and thus better inform habitat management (McGreer et al. 2015, DeMars et al. 2020).

Although research on eastern North America elk population dynamics, diet, and home range has increased (O'Neil and Bump 2014, Smith et al. 2019, Padilla et al. 2023), fewer studies have incorporated field data collected at known elk locations to explore factors that influence fine-scale resource selection (i.e. Montgomery et al. 2018, Duchamp et al. 2019, Brose 2021). Gathering information on fine-scale habitat characteristics such as plant species composition or density can help researchers further understand elk behaviors. For example, fine-scale mechanisms of plant phenology, quality, and abundance predicted landscape-scale resource selection of migratory elk in Alberta (Hebblewhite et al. 2008). Similarly, a study of elk winter foraging in Yellowstone National Park demonstrated that elk adjusted their foraging activities based on fine-scale habitat structure (Fortin et al. 2005). Indeed, fine-scale studies have provided managers with insight regarding important aspects of elk ecology in eastern North America such as parturition sites (Duchamp et al. 2019), diet composition (Smith et al. 2018), and forage availability (Lupardus et al. 2011), that could not have been obtained via coarse-scale studies. To date, few studies in eastern North America have incorporated fine-scale vegetation data collected at locations used by elk fitted with GPS collars (Smith et al. 2019) and such studies are needed to provide insight into the ecology of elk foraging behavior and response to land management activities. This is especially true in landscapes wherein important resources are patchily distributed with a matrix of relatively low-quality conditions and at scales that are finer than what can be detected using broader cover type designations (McCann et al. 2014). The failure to recognize such relationships has the potential to result in less effective habitat management recommendations.

We conducted on-the-ground vegetation surveys at used GPS elk locations and available (random) locations in Pennsylvania, USA, to identify fine-scale factors that influence seasonal resource selection by an elk population inhabiting a heavily forested portion of the central Appalachians Mountains. The notion of elk being intermediate grazers is common in the literature (Cook 2002), therefore during the spring and summer seasons, we predicted that elk would prioritize herbaceous forage acquisition and be near forest-open ecotones. Elk are known to use mast as a food source during fall (Lupardus et al. 2011), therefore we predicted that in fall elk would select for areas with higher basal areas of mast-producing trees such as oaks *Quercus*, American beech *Fagus grandifolia*, and hickories *Carya*, prioritize herbaceous forage acquisition, and be near forest–open ecotones. During winter, we predicted elk would prioritize thermoregulation (i.e. use conifers for cover) by being in or near mixed or evergreen forests and also prioritize herbaceous forage acquisition during a period of low food availability (Christianson and Creel 2007). Additionally, we analyzed plant species occurrence data at locations where elk were presumably foraging, to identify species indicative of areas used by elk to inform more detailed management practices. Findings from our study along with those from a concurrent landscape-scale study (Padilla et al. 2023) provide a more holistic assessment of elk resource selection than previously available to agency biologists and land managers. Moreover, this study can serve

as a model for others who desire to explore fine-scale influence of ungulate ecology.

Study area

We conducted our study within the Pennsylvania Elk Management Area (EMA) in northcentral Pennsylvania, located within the central Appalachian Mountains. The EMA encompasses 973 100 ha (9713 km^2) and consists of private (26%) and public land (74%) including state game lands (SGL), state forests (SF), and state parks (Banfield and Rosenberry 2020). The elevation of the EMA ranges from 267 to 732 m and this area experiences cold winters (mean January temperature is −3°C) and warm summers (mean July temperature is 22°C) (Padilla et al. 2023). Mature northern hardwood and oak–hickory forests make up 87% of the EMA and are dominated by American beech *Fagus grandifolia*, maples *Acer* spp., oaks *Quercus* spp., birch *Betula* spp., and hickory *Carya* spp. (Banfield and Rosenberry 2020). The EMA is composed of 8% herbaceous-dominated communities which include reclaimed surface mine lands, fields maintained specifically for wildlife, utility corridors, and agriculture. These cover types consist of various grasses such as timothy *Phleum pratense*, orchardgrass *Dactylis glomerata*, and fescues (*Festuca* spp.), and forbs such as goldenrods (*Solidago* spp.), clovers (*Trifolium* spp.), bird's foot trefoil *Lotus corniculatus*, and purple-crown vetch *Securigera varia* (Heffernan 2009, Banfield and Rosenberry 2020). At the time of this study, Pennsylvania's elk population consisted of approximately 1300 individuals that occupied roughly one-third of the EMA; therefore, this research was restricted to three public land blocks managed by the Pennsylvania Game Commission (PGC) and the Department of Conservation and Natural Resources (DCNR) (Fig. 1) (hereafter focal landscapes) in the core EMA. These focal landscapes are representative of the cover types and topography available to elk across the EMA (Table 1) and were chosen to maximize survey effort and inform future implementation of habitat management on public lands. Collectively, the three focal landscapes total 96 400 ha and consist of mixed hardwoods, dry oak–heath forests, northern hardwoods, reclaimed surface mines, and managed herbaceous areas (Banfield and Rosenberry 2020).

Material and methods

Fine-scale vegetation sampling

We obtained location data from 39 adult elk (female = 23, male = 16) marked with Vertex Plus Iridium collars (Vectronic Aerospace, Berlin, Germany, 8–15 m resolution) between 1 April 2021 and 31 August 2022 which were programmed to acquire a location every 13 h. Elk were captured by Pennsylvania Game Commission staff in accordance with standard procedures to capture, handle, and fit GPS collars on elk (PGC SOP 40.9). To identify potential sampling locations, we obtained GPS location data (hereafter 'used

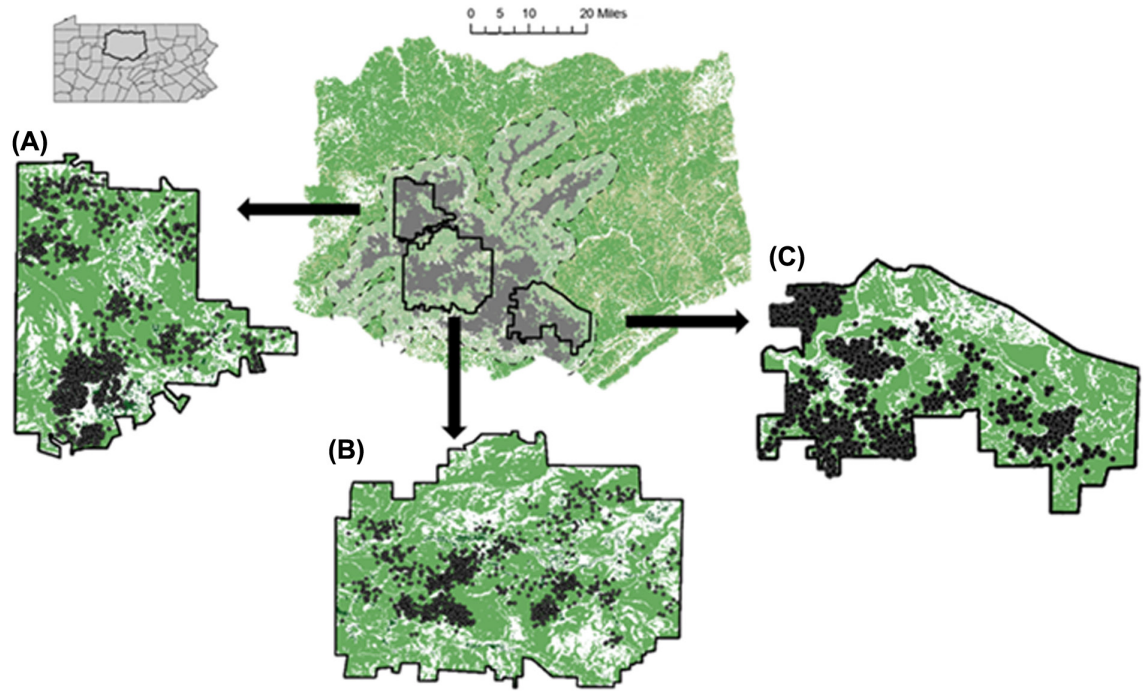


Figure 1. The Pennsylvania Elk Management Area (EMA) in northcentral Pennsylvania. The dashed black line encompasses the portion of the EMA currently occupied by elk and the three polygons with solid black outlines represent three focal landscapes (A–C) in which fine-scale habitat selection of GPS-collared elk was studied. Within each focal landscape vegetation was sampled from April 2021 to August 2022 at locations used by elk (black dots).

Table 1. Landscape attribute descriptions of the Pennsylvania Elk Management Area (EMA), occupied elk range, and focal landscapes. Focal landscapes represent where vegetation surveys were conducted at locations used by GPS-collared elk and paired available locations. Vegetation surveys were conducted from April 2021 to August 2022.

Landscape attribute	Pennsylvania EMA	Occupied elk range	Focal landscape A	Focal landscape B	Focal landscape C
Area (ha)	973 306	343 603	18 313	46 748	343 956
Elevational range (m)	154–787	199–737	268–719	255–720	217–722
Forest cover (%)	88.98	92.5	93.67	97.16	94.51
Herbaceous cover (%)	6.15	3.4	3.2	0.57	2.24
Developed area (%)	4.32	3.63	3.2	2.24	2.77
Water (%)	0.52	0.44	0.02	0.02	0.45

locations') from collared elk every two weeks. From the pool of all used locations, we randomly selected 30 used locations in each focal landscape. Additionally, for each used location we generated 2–3 random (hereafter 'available') locations using the geoprocessing tool ModelBuilder (ArcGIS Pro 2.8.3). We generated three available locations for every used location in spring and summer 2021, but due to time and resource constraints we only generated two available locations for every used location for the remainder of the study. All available locations were generated within 900 m of their respective used location. We used a 900-m distance because it is the average step-length for collared elk with 13-h fix rates in the study area (B. J. Padilla, unpubl.).

We conducted vegetation surveys at used and available locations from April 2021 and August 2022 during four relevant seasons determined by local climate and elk biology (Duchamp et al. 2019, Padilla et al. 2023): spring (1 April–31 May), summer (1 June–31 August), fall (1 September–30 November), and winter (1 December–31 March). We completed all vegetation surveys within 16 (± 6) days of a given location's acquisition date to ensure vegetation characterization was synchronous with the time the elk used the location. Plant community composition data were recorded for the herbaceous layer, small woody stems (< 10 cm diameter at breast height), and trees for each plot. To characterize the ground layer, we visually estimated percent ground cover of grass, forbs, ferns, and woody stems < 0.5 m tall using five cover classes (1: > 0–5%, 2: 6–25%, 3: 26–50%, 4: 51–75%, 5: 76–100%) in five 1 m^2 quadrats located at the center of each sampling location and at 10 m in each cardinal direction (Fig. 2). When possible, we attempted to identify all plants to the species level but sometimes could only determine genus or family. Percent cover estimates were determined as if a species or functional group (i.e. grasses) were the only plant in the quadrat (adapted from Smith et al. 2018). We did not record percent ground cover if the snow depth was > 0.25 m unless plant material was exposed above the snow. To assess woody stem density, we recorded the species name and number of all saplings and shrubs (> 0.5 m in height) within a 20 m long × 1 m wide belt transect that was oriented north to

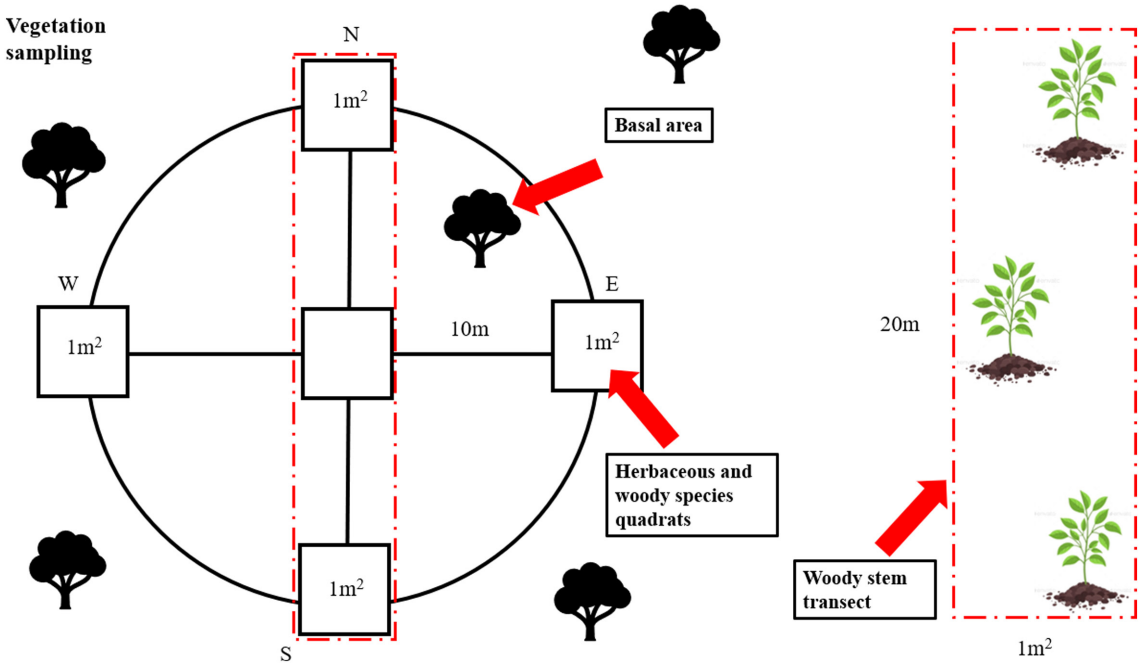


Figure 2. Diagram of vegetation survey layout conducted at used and available sampling locations to analyze elk resource selection in north-central Pennsylvania. Surveys included using a 10-factor prism to determine basal area, five 1 m^2 quadrats for percent cover of plant species, and a 1 × 20 m^2 transect to determine the number of stems of saplings and shrubs > 0.5 m.

Table 2. Candidate model sets by season to test with conditional logistic regressions to evaluate seasonal resource selection of GPS-collared elk in northcentral Pennsylvania. Elk locational data and field vegetation data were collected from April 2021 to August 2022.

Season	Variables	K	Delta_AICc	AICcWt
Spring	basal area, distance^2, graminoid	4	0.00	0.20
	basal area, distance^2	3	0.05	0.20
	basal area, distance^2, forb	4	0.45	0.16
	basal area, distance^2, graminoid, forb	5	1.02	0.12
	basal area, graminoid	2	1.37	0.10
	basal area	1	1.89	0.08
	basal area, forb	2	2.00	0.07
	basal area, graminoid, forb	3	2.24	0.07
	distance^2, graminoid, forb	4	47.27	0.00
	distance^2, graminoid	3	48.19	0.00
	distance^2, forb	3	57.86	0.00
	distance^2	2	62.73	0.00
	graminoid, forb	2	69.43	0.00
	graminoid	1	71.31	0.00
	forb	1	91.07	0.00
Summer	basal area, distance^2, graminoid, forb	5	0.00	0.39
	basal area, distance^2, graminoid	4	0.86	0.25
	basal area, distance^2, forb	4	0.87	0.25
	basal area, distance^2	3	3.73	0.06
	basal area, graminoid, forb	3	5.96	0.02
	basal area, graminoid, forb	2	6.96	0.01
	basal area, forb	2	8.01	0.01
	basal area	1	11.49	0.00
	distance^2, graminoid, forb	4	76.63	0.00
	distance^2, graminoid	3	78.85	0.00
	distance^2, forb	3	89.11	0.00
	distance^2	2	97.99	0.00
	graminoid, forb	2	116.61	0.00
	graminoid	1	119.81	0.00
	forb	1	140.09	0.00
Fall model set 1	basal area, graminoid, forb	3	0.00	0.36
	basal area, graminoid	2	0.88	0.23
	basal area, graminoid, forb, distance	4	0.90	0.23
	basal area, graminoid, distance	3	1.89	0.14
	basal area, forb	2	5.26	0.03
	basal area, forb, distance	3	6.24	0.02
	basal area	1	9.42	0.00
	basal area, distance	2	10.59	0.00
	graminoid, forb	2	32.18	0.00
	graminoid, forb, distance	3	33.90	0.00
	graminoid	1	37.90	0.00
	graminoid, distance	2	39.22	0.00
	forb	1	47.67	0.00
	forb, distance	2	48.85	0.00
	distance	1	63.29	0.00
Fall model set 2	ba_mast, forb, graminoid	3	0.00	0.54
	ba_mast, distance, graminoid, forb	4	0.81	0.36
	ba_mast, graminoid	2	5.18	0.04
	ba_bast, distance, graminoid	3	6.23	0.02
	graminoid, forb	2	6.62	0.02
	distance, gramnoid, forb	3	7.71	0.01
	ba_mast, forb	2	11.59	0.00
	graminoid	1	11.71	0.00
	ba_mast, distance, forb	3	12.47	0.00
	distance, graminoid	2	13.03	0.00
	forb	1	21.48	0.00
	distance, forb	2	22.66	0.00
	ba_mast	1	24.67	0.00
	ba_mast, distance	2	25.99	0.00
	distance	1	37.10	0.00

(Continued)

Table 2. Continued.

Season	Variables	K	Delta_AICc	AICcWt
Winter	basal area, graminoid, forb	3	0.00	0.69
	basal area, graminoid, forb, distance_con	4	2.00	0.25
	basal area, graminoid	2	5.87	0.04
	basal area, graminoid, distance_con	3	7.84	0.01
	basal area, forb	2	9.09	0.01
	basal area, forb, distance	3	10.91	0.00
	basal area	1	17.86	0.00
	basal area, distance_con	2	19.71	0.00
	graminoid, forb	2	31.31	0.00
	graminoid, forb, distance_con	3	33.24	0.00
	graminoid	1	41.20	0.00
	graminoid, distance_con	2	43.06	0.00
	forb	1	52.82	0.00
	forb, distance_con	2	54.64	0.00
	distance_con	1	72.01	0.00

[2] quadratic term.

south through the plot center. We used a 10-factor prism at plot center to tally the number of 'in-trees' and subsequently estimate basal area (m^2/ha).

Resource selection

We developed four a priori candidate models to evaluate seasonal elk resource selection. We used conditional logistic regression to evaluate resource selection such that each paired set of used and available locations were conditional strata, using the function *clogit* in the R package 'survival' (Therneau 2024). We pooled individual elk IDs within each conditional-logistic model to account for non-independence of observations from each individual using the 'cluster' argument. When developing model sets, we expected that an intermediate (quadratic) value may be important during selection (Signer et al. 2019). With that in mind, we ran likelihood ratio tests ($p \leq 0.05$) for the distance to forest–open ecotone variable to assess whether a linear or quadratic term would best represent this variable in our models. Multicollinearity of variables was tested using Pearson's correlation coefficient and variance inflation factor (VIF). Models were ranked using AIC_c where values < 2.00 from the top model were considered equivalent competing models (Burnham and Anderson 2015).

To evaluate seasonal patterns of resource selection we analyzed separate model sets for each season in response to combinations of four habitat covariates: two binary measures of elk foraging resources – presence of forbs, and presence of graminoids; and two measures of secure cover used by elk for resting and ruminating – distance to forest–open ecotone, and total tree basal area (m^2/ha). We considered forbs and graminoids to be present at a given location if they were observed in at least one of the five 1 m^2 sampling quadrats. For both spring and summer analyses, model sets contained the variables total basal area (m^2/ha), the quadratic term for distance to a forest–open ecotone (m), and presence of forbs and graminoids (Table 2). To analyze fall elk resource selection, we analyzed two model sets. Model set one included the variables total basal area, presence of forbs, presence of graminoids, and distance to a forest–open ecotone. Model set two included the same variables as model set one except only it analyzed the basal area of mast-producing trees *Quercus*, *Fagus*, *Carya* (m^2/ha), because mast has been shown to be a component of elk diets during the fall (Heffernan 2009, Lupardus et al. 2011) (Table 2). Finally, during the winter, elk must prioritize thermoregulation and forage acquisition during a time of low food availability (Christianson and Creel 2007). Therefore, the candidate model set to analyze elk resource selection in the winter included total basal area (m^2/ha), presence of forbs and graminoids, and distance to a conifer/mixed cover forest type (Table 2). Total basal area was log transformed to improve normality. All continuous covariates were scaled separately for each season ($\bar{x} = 0$, $SD = 1$) prior to conducting analyses. All sampling locations that did not have a complete set of paired used or available surveys due to field logistics (i.e. access) were removed from the analysis.

We used the 2019 National Land Cover Database (Dewitz 2021, 30 m resolution) in ArcGIS Pro 2.8.3 (ESRI 2021) to quantify distance edges between open-canopied herbaceous communities and closed-canopy forests to define ecotone boundaries. To do this, we classified deciduous forest [NLCD-41], mixed forest [NLCD-43], evergreen forest [NLCD-42], scrub/shrub [NLCD-52], and woody wetlands [NLCD-90] into a single cover type called 'forest'. We reclassified emergent herbaceous wetlands [NLCD-95], cultivated crop [NLCD-82], grassland herbaceous [NLCD-71], hay/pasture [NLCD-81], and barren land [NLCD-31] into a single cover type called 'herbaceous'. Conifers are an important habitat component for elk during winter (Padilla et al. 2023), therefore we combined evergreen [NLCD-42] and mixed forests [NLCD-43] for analysis of winter resource selection. The boundaries between the herbaceous and forested cover types were defined as the intersection of the newly created polygons ('forest' and 'herbaceous'), hereafter referred to as ecotones, and the distance between these polygons was generated using the tool generate near table (ESRI 2021).

Indicator species

Finally, we used multivariate correlation indices to compare vegetation species recorded in the 1 m^2 quadrants at used and available locations associated with peak foraging times. We defined peak foraging locations as those that were acquired between 30-min pre-sunrise to 150-min post-sunrise and 60-min pre-sunset to 120-min post-sunset (6 h total; adapted from Johnson et al. 2000, Roberts et al. 2017). Plants species or groupings that averaged less than five percent cover and species or groups that occurred in less than one percent of sampling locations were not included in this analysis. Similarly, several species were grouped based on genus and family (e.g. cinquefoils, trifoliums, goldenrods) for more concise results that can be easily interpreted by land managers. Female and male locations were lumped due to finding few differences between the sexes (Verch 2023). To determine indicator species of herbaceous plants and woody stems < 0.5 m found in 1 m^2 quadrants at locations used by elk, and areas available but unused during foraging periods (hereafter referred to as site groups), the diagnostic index IndVal from package 'indicspecies' (Dufrene and Legendre 1997) was calculated to assess species association between site groups. These values were derived from the absolute abundance of individual and groups of species to estimate the probability of a plant belonging to a specific site group as well as the relative frequency of occurrence within the site group (De Cáceres and Legendre 2009). These values are useful to characterize plant communities by taxa (i.e. species found in managed openings, disturbed areas) that reflect where elk are located during periods of foraging. Indicator values were tested with Monte Carlo randomization and were considered significant if $p < 0.05$. All data were analyzed using program R ver. 4.1.1 via Rstudio (www.r-project.org).

Results

Conditional logistic regressions

We completed 3803 vegetation surveys at 1294 used and 2509 available locations from 39 individuals (23 females; 16 males) across four seasons from April 2021 to August 2022. In spring (291 used; 601 available), the top model (AICwt = 0.20) for selection included total basal area (m^2/ha), the quadratic term for distance to a forest–open ecotone (m), and graminoid presence (Table 2). The probability of use by elk decreased as total basal area (m^2/ha) increased ($\beta = -0.66$, SE: 0.1) (Fig. 3) and increased with the presence of graminoids ($\beta = 0.31$, SE = 0.21). The log odds ratio indicated that likelihood of use decreased 51% for every 6.7 m^2/ha increase in total basal area and increased 36% with the presence of graminoids. There was a weak ($p = 0.07$) quadratic relationship with elk use and distance to a forest–open ecotone with the top model; however, the second competing

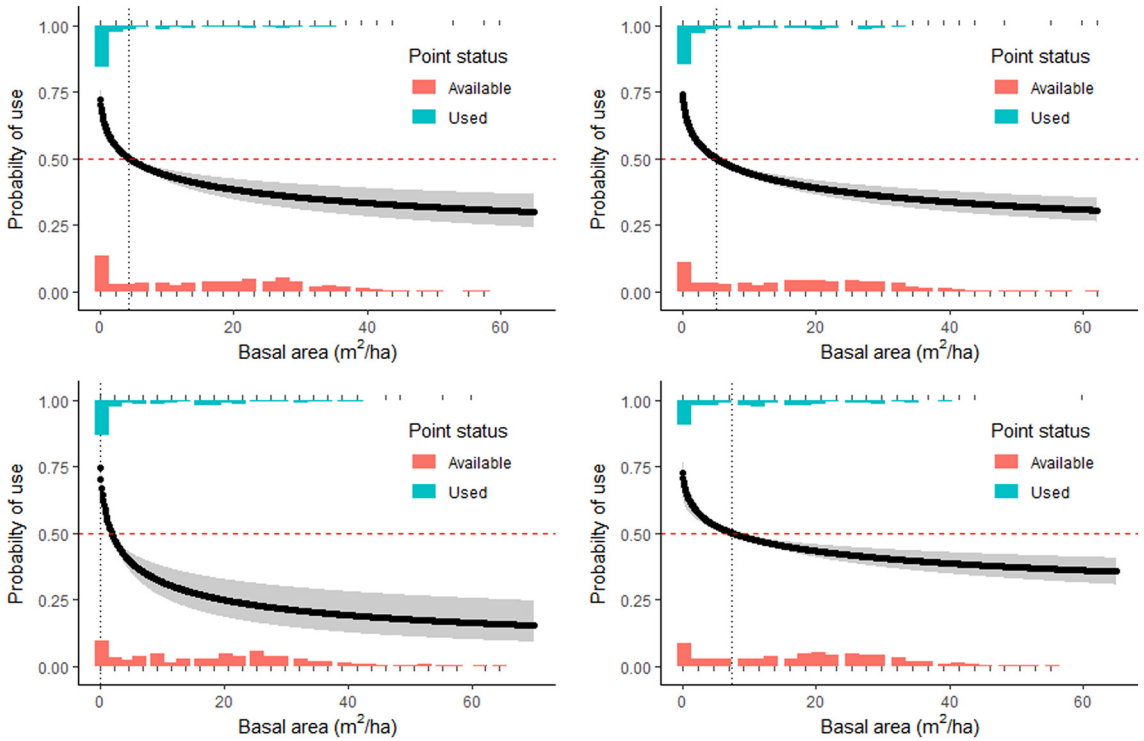


Figure 3. Seasonal probability of use by elk with total basal area from the top-ranked models using conditional logistic regressions comparing elk resource selection at used (n = 792) and available (n = 1529) locations from April 2021 to August 2022. Spring: 1 April–31 May, summer: 1 June–31 August, fall: 1 September–30 November, and winter: 1 December–31 March. Note: For each figure the light gray shading represents the 95% confidence intervals and the black dotted vertical line represents predicted covariate values at 0.5 probability of use by elk (red dashed line).

model (dAIC = 0.05) which included basal area (m^2/ha) and the quadratic term for distance to a forest–open ecotone (m), found that distance to a forest–open ecotone (β = −0.42, SE = 0.19) had a significant negative effect on probability of use. The log odds ratio indicated that likelihood of use decreased by 35% for every 291 m from a forest–open ecotone. While basal area was the driving variable for resource selection in the spring, there were five other competing models (dAIC = 0.45, 1.02, 1.37, 1.89, 2.00) which included two additional variables of presence of forbs and presence of graminoids (Table 2). In summer (463 used; 889 available), the best-supported model (AICwt = 0.39) included total basal area (m^2/ha), the quadratic term for distance to a forest–open ecotone (m), presence of forbs, and presence of graminoids (Table 2). The probability of use by elk decreased as total basal area (m^2/ha) (β = −0.65, SE = 0.08) (Fig. 3) increased and distance to forest–open ecotone increased (Linear: β = −0.51, SE = 0.16, Quadratic = β = 0.13, SE = 0.06). The log odds ratio indicated that the likelihood of use decreased by 48% for every 6.1 m^2/ha increase in total basal area, and decreased by 40% as distance to a forest–open ecotone increased every 352 m. The log odds ratio also indicated that the likelihood of use increased by 32 and 50% with the presence of graminoids and forbs, respectively. There were two competing models (dAIC = 0.86, 0.87), both with basal area providing the most information on summer resource selection with no additional variables. The best-supported model for fall model set one (240 used; 438 available) (AICwt = 0.36) included variables total basal area, presence of forbs, and presence of graminoids, with basal area as the driving factor for resource selection. The probability of elk use decreased as total basal area increased (β = −0.67, SE = 0.11) (Fig. 3) but increased with the presence of forbs (β = 0.35, SE = 0.24) and graminoids (β = 0.63, SE = 0.24). The log odds ratio indicated that the likelihood of use decreased by 45% for every 14.3 (m^2/ha) increase of total basal area and increased by 49 and 88% with the presence of forbs and graminoids, respectively. Two competing models (dAIC = 0.88, 0.90) had no additional variables. However, a third competing model (dAIC = 1.89, Table 2) included distance to a forest ecotone but was considered to have a weak biological effect. The best-supported model (AICwt = 0.54) for fall model set two (240 used; 438 available) included basal area of mast-producing trees (m^2/ha), presence of forbs, and presence of graminoids (Table 2). The probability of elk use decreased as basal area of mast-producing trees increased (m^2/ha) (β = -0.30, SE = 0.10) (Fig. 3) and increased with the presence of forbs (β = 0.59, SE = 0.23) and graminoids (β = 0.82, SE = 0.23). The log odds ratio indicates the likelihood of use decreased by 28% for every 5.9 m^2/ha increase of basal area of mast-producing trees and use increased 81 and 126% with the presence of forbs and graminoids, respectively. The competing model (dAIC = 0.81) only included one new variable: distance to forest–open ecotone (m), which was considered to have a weak biological effect (Table 2). Finally, for winter selection (300 used; 581 available) the top model (AICwt = 0.69) included total basal area (m^2/ha), presence of forbs, and presence of graminoids. Probability of use by elk decreased as total basal area (m^2/ha) increased (Fig. 3) (β = −0.49, SE = 0.09) and increased with the presence of forbs (β = 0.57, SE = 0.2) and presence of graminoids (β = 0.62, SE = 0.19). The log odds ratio indicated that the likelihood of elk use decreased by 39% for every 4.9 m^2/ha increase in basal area (Fig. 3) and increased by 77% and 87% with the presence of forbs, and graminoids, respectively. There was only one competing model, which included the same three variables from the top model and distance to a forest–open ecotone (β = −0.49, SE = 0.09), but was considered to have a weak biological effect.

Species indicator

Indicator species analysis revealed several plant species and genera differences between peak foraging used (n = 792) and available (n = 1529) locations. In this context, indicators of used locations were representative of the plant communities elk selected for during presumed foraging periods, while available locations reflected species elk most likely did not use. During spring, seven genera: clovers *Trifolium*, chickweeds/mouse-eared chickweeds (*Stellaria* and *Cerastium*), plantains *Plantago*, thistles *Cirsium*, speedwells *Veronica*, wintercress *Barbarea* and four species: common dandelion *Taraxacum officinale*, purple crownvetch *Securigera varia*, bird's-foot trefoil *Lotus corniculatus*, and ox-eye daisy *Leucanthemum vulgare* were indicators of used locations (Table 3). Three species: starflower *Trientalis borealis*, black birch seedlings *Betula nigra*, and fringed polygala *Polygala paucifolia*, were indicative of available locations during spring (Table 3). Nine genera were indicators of used summer locations: clovers, plantains, thistles, wood sorrels *Oxalis*, knotweeds *Persacaria*, chickweeds/mouse-eared chickweed, sweet clovers *Melilotus*, and American asters *Symphyotrichum* and eight species: common dandelion, black medick *Medicago lupulina*, wild carrot *Daucus carota* (IV: 67%, p = 0.002), common ragweed *Ambrosia artemisiifolia*, sheep sorrel *Rumex acetosella,* fireweed *Chamaenerion angustifolium*, Carolina horsenettle *Solanum carolinense*, common milkweed *Asclepias syriaca* (Table 3). Three species: black birch seedlings, wild sarsaparilla *Aralia nudicaulis*, and American beech seedlings *Fagus grandifolia* were indicative of available locations during summer (Table 2). Indicators of locations used during fall included eight genera: clovers, plantains, thistles, speedwells, wood sorrels, knotweeds, chickweeds/mouse-eared chickweed, and American asters, and three species: common dandelion, sheep sorrel, and common milkweed (Table 3). No species or genera were indicators of available locations during the fall (Table 3). One genus: clovers, and one species: common dandelion were indicative of locations used by elk during winter. Barren strawberry *Waldsteinia fragarioides* was an indicator of available locations during winter (Table 3). It is important to note that summer may have more species indicators due to the flowering plants being easier to identify compared to spring, fall, and winter.

Table 3. Results from the species indicator analysis for herbaceous and < 0.5 m woody stems genera/species. Vegetation data were sampled at locations used by GPS-collared elk (n = 39) or available to elk (within 900 m of used location) from April 2021 to 31 August 2022 in northcentral Pennsylvania. A = Sample probability of species belonging to a used or available location. B = Sample estimate probability of finding species at a used or available location. Stat = IndVal index.

	Used				Available				
Season	Species/Group	A	B	stat	p-value	Group	A	B	stat	p-value
Spring	*Trifolium*	0.78	0.31	0.494	0.001	*Trientalis borealis*	0.92	0.07	0.25	0.005
	Taraxcum officinale	0.84	0.23	0.441	0.001	*Betula lenta* seedlings	0.98	0.06	0.245	0.002
	Securigera varia	0.79	0.18	0.38	0.001	*Polygala paucifolia*	1	0.02	0.165	0.035
	Stellaria, Cerastium	0.8	0.15	0.349	0.001					
	Plantago	0.81	0.13	0.328	0.001					
	Lotus corniculatus	0.71	0.13	0.307	0.003					
	Cirsium	0.73	0.13	0.304	0.001					
	Veronica	0.6	0.08	0.218	0.036					
	Barbarea	0.86	0.05	0.202	0.008					
	Leucanthemum vulgare	0.87	0.031	0.166	0.013					
Summer	*Trifolium*	0.88	0.35	0.556	0.001	*Betula lenta* seedlings	0.83	0.06	0.227	0.008
	Securigera varia	0.73	0.22	0.404	0.001	*Aralia nudicaulis*	1	0.4	0.19	0.003
	Plantago	0.81	0.17	0.369	0.001	*Fagus grandifolia*	0.89	0.3	0.176	0.015
	Taraxcum officinale	0.8	0.16	0.354	0.001					
	Circisum	0.85	0.12	0.325	0.001					
	Oxalis	0.78	0.11	0.297	0.001					
	Medicago lupulina	0.67	0.11	0.275	0.002					
	Daucus carota	0.71	0.09	0.259	0.005					
	Ambrosia artemisiifolia	0.89	0.05	0.222	0.001					
	Persicaria	0.68	0.07	0.215	0.001					
	Rumex acetosella	0.78	0.06	0.214	0.001					
	Chamaenerion angustifolium	0.64	0.07	0.209	0.026					
	Stellaria, Cerastium	0.78	0.05	0.201	0.001					
	Melilotus	0.85	0.04	0.181	0.004					
	Solanum carolinense	0.8	0.03	0.161	0.007					
	Symphyotrichum	0.79	0.03	0.16	0.026					
	Asclepias syriaca	0.78	0.03	0.16	0.038					
Fall	*Trifolium*	0.83	0.29	0.495	0.001	None				
	Taraxcum officinale	0.91	0.14	0.363	0.001					
	Plantago	0.86	0.14	0.346	0.001					
	Cirsium	0.93	0.1	0.306	0.001					
	Rumex acetosella	0.74	0.08	0.248	0.002					
	Veronica	0.86	0.07	0.244	0.002					
	Oxalis	0.84	0.05	0.206	0.017					
	Persicaria	0.81	0.04	0.19	0.037					
	Potenilla	0.77	0.04	0.184	0.045					
	Stellaria, Cerastium	0.86	0.04	0.18	0.043					
	Symphyotrichum	0.84	0.03	0.163	0.043					
	Asclepias syriaca	1	0.02	0.137	0.045					
Winter	*Trifolium*	0.74	0.13	0.315	0.015	*Waldsteinia fragarioides*	1	0.037	0.193	0.021
	Taraxcum officinale	0.73	0.05	0.194	0.041					

Discussion

This study provides one of the first assessments of fine-scale resource selection of GPS collared elk in eastern North America. In all seasons, elk selected areas with low tree cover and more herbaceous plants, reiterating the critical importance of open cover types with ample forage for elk, particularly in heavily forested landscapes. The positive association between herbaceous cover and elk has been observed in landscape scale studies both in Pennsylvania (Padilla et al. 2023) and elsewhere across the species range (Anderson et al. 2005b, Smith et al. 2019). In a recently translocated population in the Missouri Ozarks, elk resource selection was similarly influenced by forage openings such as glades and grasslands (Smith et al. 2019). Female elk in South Dakota and Pennsylvania have also been shown to select parturition sites near herbaceous openings with ample forage to fulfill high energetic needs (Lehman et al. 2016, Duchamp et al. 2019). Additionally, we found distance to a forest–open ecotone to only have a strong biological effect in spring but was still an important variable for top models in summer and fall. Other studies reported the use of forest edge by elk for security cover (Boyce et al. 2003, Rumble and Gamo 2011, O'Neil and Bump 2014), where in areas with high predation, the use of ecotones by elk help balance both their nutritional and security needs (Boyce et al. 2003, Mao et al. 2005). While adult elk in

Pennsylvania are not subject to high predation rates, predation of calves occurs by black bears and coyotes (Corondi 2023), and forest edges for security cover adjacent to herbaceous forage influenced the selection of parturition sites by female elk in Pennsylvania (Duchamp et al. 2019). While informative, analyses that only incorporate remote-sensed environmental data are limited in their ability to identify the fine-scale factors that are important drivers of animal movement and resource selection (Briand et al. 2009). Indeed, results from our analyses that included both remotely sensed (e.g. distance to an ecotone) and micro-habitat covariates such as basal area and plant species composition provide a better understanding of the ecological contexts that drive elk resource selection in our study region. Such information provides land managers with more precise target values for vegetation characteristics when developing and implementing practices intended to replicate conditions selected for by elk.

Our results revealed that regardless of season, elk avoided areas with high tree cover and selected for those with highly nutritious and palatable graminoids and forbs. Evidence provided by fecal analyses has also revealed that elk in several eastern populations select herbaceous resources during all seasons (Schneider et al. 2006, Heffernan 2009, Lupardus et al. 2011, Smith et al. 2018). For example, graminoids comprised 65.9% of elk winter diets in Tennessee (Lupardus et al. 2011) and cool-season grasses were highly selected by elk in Missouri (Smith et al. 2018). Furthermore, a previous fecal-based study in Pennsylvania found graminoids comprised 16% and 46% of elk diets during the winter and spring, respectively (Heffernan 2009). The importance of forbs and graminoids is supported by our indicator species analysis which found that in all seasons, graminoids and forbs were indicators of locations used by elk, highlighting the value of herbaceous openings.

Many state agencies in the eastern USA promote permanent herbaceous openings to provide quality forage opportunities for elk throughout the year (Minnesota Department of Natural Resources 2016, Banfield and Rosenberry 2020, Brose 2021). This includes the creation and maintenance of managed herbaceous openings that are often planted with a variety of graminoids and forbs (Jones 2014, Brose 2021). Importantly, while managed herbaceous openings only represented 2% of our three focal landscapes, 37% of the areas used by elk that we surveyed were in agency-managed herbaceous openings planted with a mixture of clovers *Trifolium repens*, *T. pratense*, various warm season and cool season grasses (*Phleum pratense*, *Lolium* spp.), and legumes *Lotus corniculatus*. Moreover, an additional 16% of locations used by elk that we sampled were within 100 m of agency-managed herbaceous openings. The use of herbaceous openings are not uncommon among eastern elk populations occupying forest-dominated landscapes, for instance, elk in Missouri were found to have a strong selection for managed herbaceous openings (Pero et al. 2023), and diets of elk contained several herbaceous species from reclaimed surface mine lands in Tennessee and Kentucky (Schneider et al. 2006, Lupardus et al. 2011).

Our fine-scale resource selection study allowed us to delve deeper into species composition of areas used and available to elk, specifically managed herbaceous plots, whereas such data are often not obtainable from higher (30 × 30 m) resolution data. Results from the species indicator analysis are further indicative of elk using areas hosting plant species found in managed openings. In particular, clover species were indicators of locations used by elk in every season, and clovers have been documented in elk diets in Missouri, Tennessee, and Kentucky (Schneider et al. 2006, Lupardus et al. 2011, Smith et al. 2018). Purple crownvetch *Securigera varia*, bird's-foot trefoil *Lotus corniculatus*, black medick *Medicago lupulina*, sheep's sorrel *Rumex acetosella*, and other forbs were also indicators of areas used by elk in our study, and are representative of herbaceous openings managed by PGC and DCNR (Banfield and Rosenberry 2020). The identification of specific plant species that are indicative of locations used by elk can be informative to managers when implementing the creation or maintenance of herbaceous openings. Additionally, species that were found to be indicators of available locations included fringed polygala *Polygala paucifolia*, starflower *Trientalis borealis*, and beech seedlings *Betula lenta*. These species are commonly found in closed-canopy forests, indicating that during foraging periods, elk are not using areas with these plants compared to their availability, and thus managers should not consider these species as preferred foraging options for elk. Results from our resource selection and indicator species analyses stress the importance of managed herbaceous areas to elk in Pennsylvania's heavily forested EMA. Importantly, selection of a particular resource does not necessarily equate to better survival or reproduction. However, if a management goal is to expand the current occupied elk range, our results suggest that the creation and maintenance of herbaceous communities in areas currently lacking these conditions would likely increase elk foraging opportunities and thus facilitate expansion.

It is important to also consider the disadvantages associated with ongoing management of herbaceous openings. Public land managers and private landowners regularly invest significant time, money, and effort creating and maintaining herbaceous openings through discing, fertilizing, spraying, planting, and prescribed burns (Banfield and Rosenberry 2020, Brose 2021). A drawback to planting often includes the use of non-native forage species. These can contribute to widespread naturalization of invasive plants (Litt and Pearson 2013). Many non-native forage species (e.g. purplecrown vetch, bird's-foot trefoil) were found to be indicators of elk locations in our species indicator analysis. Despite the continued use of managed food plots, a study on the value of permanent forest openings conducted in Wisconsin found that enhanced wildlife openings did not appear to provide better forage compared to young forest patches, and that use of other herbaceous openings such as utility lines and road edges provided quality forage to elk (Brose 2021). Indeed, we found native plants indicative of elk used locations including fireweed *Chamaenerion angustifolium*, asters *Symphyotrichum* spp., and speedwells *Veronica* spp., which supports the idea that elk are generalist foragers that will take advantage of most graminoids and forbs when available, particularly plants rich in dietary protein (Cook 2002). Nearly half (47%) of

locations used by elk that we sampled were ≥ 100 m from managed herbaceous openings, which reveals the importance of other cover types to elk including forests (both mature and regenerating timber harvests) and open areas including rights-of-way, reclaimed surface mines, and old fields. Our results support elk use of open community types not specifically managed for the species and can help guide management practices intended to increase foraging opportunities.

Because our RSFs revealed tree density as the driving factor of resource selection during all seasons, along with the selection of herbaceous areas, managing for open woodlands could be an alternative to managed herbaceous openings. Oak woodlands and savannahs were historically abundant in the eastern USA but have become rare in contemporary landscapes due to lack of periodic disturbances by fire, resulting in closed canopy forest with little herbaceous forage available for elk (Hanberry et al. 2020). These fire-dependent communities are characterized by having variable tree density (50–250 trees/ha) with little to no mid-story, thus creating open canopy conditions whereby increased sunlight promotes a rich herbaceous ground layer (Hanberry et al. 2020). Efforts to restore open woodlands have begun in parts of the eastern USA (Tennessee Wildlife Resources Agency 2018). Continued creation and maintenance of these open woodlands through prescribed fire and mechanical thinning could provide ample high-quality elk forage, thereby reducing the need to create managed food plots (Hanberry et al. 2020). Indeed, it has been suggested that forests with open to moderate canopies can provide elk with both security cover and intermediate forage opportunities that allow elk to reduce movement costs (Rumble and Gamo 2011). While these open forest ecosystems require some form of successional setback (e.g. mechanical thinning, mowing, prescribed fire), ungulates can help maintain these open areas due to the browsing of small-diameter trees in canopy gaps (Hanberry and Faison 2023). Restoring open oak woodlands and similar open-canopied forest types (i.e. pitch pine–scrub oak) in heavily forested landscapes will provide sources of forage for elk, while also creating much-needed habitat for many declining species of birds (Brawn 2006, Bakermans et al. 2015), pollinators (Lee et al. 2014, Mathis et al. 2022), and mammals (Boyce and Barry 2007) that require early successional conditions (Hanberry and Thompson 2019, Bragg et al. 2020).

Our work demonstrates the importance of fine-scale studies to understand drivers of ungulate resource selection (Briand et al. 2009, Hebblewhite and Haydon 2010). Vegetation characteristics such as tree density, distance to forest–ecotone, and species-level information on herbaceous plants, better inform land management practices to benefit elk populations in heavily forested portions of eastern North America. Our results highlight the importance of managed and unmanaged herbaceous openings to elk inhabiting a heavily forested landscape. We recommend managers increase these conditions across the Central Appalachians Mountains through the creation of additional herbaceous openings and/or the restoration of open woodlands with a strong herbaceous component maintained via prescribed fire. Such actions will likely provide more forage opportunities adjacent to areas with security cover for elk.

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Author contributions

Mallory B. Verch: Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (equal); Validation (lead); Writing – original draft (lead). **Benjamin J. Padilla**: Conceptualization (equal); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Validation (equal); Writing – review and editing (lead). **Joseph E. Duchamp**: Formal analysis (supporting); Methodology (supporting); Validation (equal); Writing – review and editing (supporting). **Jeremiah E. Banfield**: Conceptualization (equal); Methodology (supporting); Resources (lead); Writing – review and editing (supporting). **Jeffery L. Larkin**: Conceptualization (lead); Funding acquisition (lead); Methodology (supporting); Project administration (equal); Supervision (lead); Validation (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5281/zenodo.13864406 (Verch et al. 2024).

References

Anderson, D. P., Turner, M. G., Forester, J. D., Zhu, J., Boyce, M. S., Beyer, H. and Stowell, L. 2005a. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. – J. Wildlife Manage. 69: 298–310.

Anderson, D. P., Forester, J. D., Turner, M. G., Frair, J. L., Merrill, E. H., Fortin, D., Mao, J. S. and Boyce, M. S. 2005b. Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. – Landscape Ecol. 20: 257–271.

Arthur, S. M., Manly, B. F. J., McDonald, L. L., Gerald, W., Arthur, S. M., Manly, B. F. J. and Garner, G. W. 1996. Assessing habitat selection when availability changes. – Ecology 77: 215–227.

Bakermans, M. H., Smith, B. W., Jones, B. C. and Larkin, J. L. 2015. Stand and within-stand factors influencing golden-winged warbler use of regenerating stands in the central Appalachian Mountains. – Avian Conserv. Ecol. 10: 10.

Banfield, J. and Rosenberry, C. 2020. Pennsylvania elk management plan (2020–2025). – Pennsylvania Game Commission.

Boyce, K. A. and Barry, R. E. 2007. Seasonal home range and diurnal movements of *Sylvilagus obscurus* (Appalachian cottontail) at Dolly Sods, West Virginia. – Northeast. Nat. 14: 99–110.
Boyce, M. and McDonald, L. 1999. Relating populations to habitats using resource selection functions. – Trends Ecol. Evol. 14: 268–272.
Boyce, M. S., Mao, J. S., Merrill, E. H., Fortin, D., Turner, M. G., Fryxell, J. and Turchin, P. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. – Ecoscience 10: 421–431.
Bragg, D. C., Hanberry, B. B., Hutchinson, T. F., Jack, S. B. and Kabrick, J. M. 2020. Silvicultural options for open forest management in eastern North America. – For. Ecol. Manage. 474: 118383.
Brawn, J. D. 2006. Restoring oak savannas on bird communities and populations. – Conserv. Biol. 20: 460–469.
Briand, Y., Ouellet, J. P., Dussault, C. and St-Laurent, M. H. 2009. Fine-scale habitat selection by female forest-dwelling caribou in managed boreal forest: empirical evidence of a seasonal shift between foraging opportunities and antipredator strategies. – Ecoscience 16: 330–340.
Brose, A. 2021. Value of permanent forest openings to Rocky Mountain elk (*Cervus canadensis*) in Wisconsin. – MSc thesis, Univ. of Wisconsin, USA.
Brown, C. L., Kielland, K., Brinkman, T. J., Gilbert, S. L. and Euskirchen, E. S. 2018. Resource selection and movement of male moose in response to varying levels of off-road vehicle access. – Ecosphere 16: 330–340.
Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical infomation–theoretic approach, 2nd edn. – Springer-Verlag.
Christianson, D. and Creel, S. 2007. A review of environmental factors affecting elk winter diets. – J. Wildl. Manage. 71: 164–176.
Cook, J. 2002. Nutrition and food. In: Towiell, D. E. and Thomas, J. W. (eds), North American elk: ecology and management. – Smithsonian Institution Press, pp. 259–349.
Corondi, A. 2023. Reproductive success, calf survival, and spatial relationships of elk in Pennsylvania. – MSc thesis, Pennsylvania State Univ., USA.
De Cáceres, M. and Legendre, P. 2009. Associations between species and groups of sites: indices and statistical inference. – Ecology 90: 3566–3574.
DeMars, C. A., Nielsen, S. E. and Edwards, M. A. 2020. Effects of linear features on resource selection and movement rates of wood bison (*Bison bison athabascae*). – Can. J. Zool. 98: 21–31.
Dewitz, J. 2021. National Land Cover Database (NLCD) 2019 products (ver. 3.0, February 2024) [Data set]. – US Geological Survey, https://data.usgs.gov/datacatalog/data/USGS:649595d8d34ef77fcb01dca1.
Duchamp, J. E., DeVivo, M. T., DeBerti, J. M., Heffernan, L. M., Kougher, J. D. and Larkin, J. L. 2019. Selection of calf bedding sites by female elk in the central Appalachian Mountains. – J. Fish Wildl. Manage. 10: 91–101.
Dufrêne, M. and Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. – Ecol. Monogr. 67: 345–366.
ESRI. 2021. 10.8.1 Documentation manual. – Wildl. Soc. Bull. 32: 158–168. https://enterprise.arcgis.com/en/server/10.8/get-started/linux/about-arcgis-server-documentation.htm.
Fleming, K. K., Didier, K. A., Miranda, B. R. and Porter, W. F. 2004. Sensitivity of a white-tailed deer habitat-suitability index model to error in satellite land-cover data: implications for wildlife habitat-suitability studies. – Wildl. Soc. Bull. 32: 158–168.
Fortin, D., Morales, J. M. and Boyce, M. S. 2005. Elk winter foraging at fine scale in Yellowstone National Park. – Oecologia 145: 335–343.
Hanberry, B. B. and Faison, E. K. 2023. Re-framing deer herbivory as a natural disturbance regime with ecological and socioeconomic outcomes in the eastern United States. – Sci. Total Environ. 868: 161669.
Hanberry, B. B. and Thompson, F. R. 2019. Open forest management for early successional birds. – Wildl. Soc. Bull. 43: 141–151.
Hanberry, B. B., Bragg, D. C. and Alexander, H. D. 2020. Open forest ecosystems: an excluded state. – For. Ecol. Manage. 472: 118256.
Hebblewhite, M. and Haydon, D. T. 2010. Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. – Phil. Trans. R. Soc. B 365: 2303–2312.
Hebblewhite, M. and Merrill, E. H. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. – Ecology 90: 3445–3454.
Hebblewhite, M., Merrill, E. and McDermid, G. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. – Ecol. Monogr. 78: 141–166.
Heffernan, L. M. 2009. Effects of age, sex, and landscape composition on seasonal diets of elk in Pennsylvania. – MSc thesis, Indiana Univ. of Pennsylvania, USA.
Hooven, N. D., Williams, K. E., Hast, J. T., McDermott, J. R., Crank, R. D., Springer, M. T. and Cox, J. J. 2024. Landscape context and behavioral clustering contribute to flexible habitat selection strategies in a large mammal. – Mamm. Res. 69: 329–343.
Jenkins, D. A., Schaefer, J. A., Rosatte, R., Bellhouse, T., Hamr, J. and Mallory, F. F. 2007. Winter resource selection of reintroduced elk and sympatric white-tailed deer at multiple spatial scales. – J. Mammal. 88: 614–624.
Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. – Ecology 61: 65–71.
Johnson, B. K., Kern, J. W., Wisdom, M. J., Findholt, S. L. and Kie, J. G. 2000. Resource selection and spatial separation of mule deer and elk during spring. – J. Wildl. Manage. 64: 685–697.
Jones, B. C. 2014. Elk habitat management. – https://www.pgc.pa.gov/Wildlife/HabitatManagement/pages/default.aspx.
Lamont, B. G., Monteith, K. L., Merkle, J. A., Mong, T. W., Albeke, S. E., Hayes, M. M. and Kauffman, M. J. 2019. Multi-scale habitat selection of elk in response to beetle-killed forest. – J. Wildl. Manage. 83: 679–693.
Lee, K. A., Huveneers, C., Gimenez, O., Peddemors, V. and Harcourt, R. G. 2014. To catch or to sight? A comparison of demographic parameter estimates obtained from mark-recapture and mark-resight models. – Biodivers. Conserv. 23: 2781–2800.
Lehman, C. P., Rumble, M. A., Rota, C. T., Bird, B. J., Fogarty, D. T. and Millspaugh, J. J. 2016. Elk resource selection at parturition sites. – J. Wildl. Manage. 80: 465–478.
Linden, D. W., Sirén, A. P. K. and Pekins, P. J. 2018. Integrating telemetry data into spatial capture–recapture modifies inferences on multi-scale resource selection. – Ecosphere 9: e002203. 10.1002/ecs2.2203.
Litt, A. R. and Pearson, D. E. 2013. Non-native plants and wildlife in the intermountain west. – Wildl. Soc. Bull. 37: 517–526.
Lupardus, J. L., Muller, L. I. and Kindall, J. L. 2011. Seasonal forage availability and diet for reintroduced elk in the Cumberland Mountains, Tennessee. – Southeast. Nat. 10: 53–74.

Manly, B., McDonald, L. I., Thomas, D. I., McDonald, T. I. and Erickson, W. P. 2002. Introduction to resource selection studies. – Kluwer Academic Publishers.
Mao J. S., Boyce, M. S., Smith, D. W., Singer, F. J., Vales, D. J., Vore, J. M. and Merril, E. H. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. – J. Wildl. Manage. 69: 1691–1707.
Mathis, C. L., McNeil, D. J., Lee, M. R., Grozinger, C. M., Otto, C. R. V. and Larkin, J. L. 2022. Can't see the flowers for the trees: factors driving floral abundance within early-successional forests in the central Appalachian Mountains. – Can. J. Forest Res. 52: 1002–1013.
McCann, N. P., Zollner, P. A. and Gilbert, J. H. 2014. Bias in the use of broadscale vegetation data in the analysis of habitat selection. – J. Mammal. 95: 369–381.
McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C. and Cushman, S. A. 2016. Multi-scale habitat selection modeling: a review and outlook. – Landsc. Ecol. 31: 1161–1175.
McGreer, M. T., Mallon, E. E., Vennen, L. M. V., Wiebe, P. A., Baker, J. A., Brown, G. S., Avgar, T., Hagens, J., Kittle, A. W., Mosser, A., Street, G. M., Reid, D. E. B., Rodgers, A. R., Shuter, J., Thompson, I. D., Turetsky, M. J., Newmaster, S. G., Patterson, B. R. and Fryxell, J. M. 2015. Selection for forage and avoidance of risk by woodland caribou (*Rangifer tarandus caribou*) at coarse and local scales. – Ecosphere 6: 1–11.
McLaren, A. A. D., Benson, J. F. and Patterson, B. R. 2017. Multiscale habitat selection by cow moose (*Alces alces*) at calving sites in central Ontario. – Can. J. Zool. 95: 891–899.
Minnesota Department of Natural Resources. 2016. Interim strategic management plan for elk, 2016–2019. – Minnesota Department of Natural Resources.
Montgomery, R. A., Redilla, K. M., Ortiz-Calo, W., Smith, T., Keller, B. and Millspaugh, J. J. 2018. Evaluating the individuality of animal–habitat relationships. – Ecol. Evol. 8: 10893–10901.
O'Neil, S. T. and Bump, J. K. 2014. Modeling habitat potential for elk expansion in Michigan, USA. – Wildl. Biol. Pract. 10: 111–131.
Padilla, B. J., Banfield, J. E., Corondi, A. and Larkin, J. L. 2023. Seasonal variation in size and composition of elk (*Cervus canadensis*) home range in central Appalachia. – Can. J. Zool. 101: 1–14.
Pero, E. M., Palm, E. C., Chitwood, M. C., Hildreth, A. M., Keller, B. J., Sumners, J. A., Hansen, L. P., Isabelle, J. L. and Millspaugh, J. J. 2023. Spatial acclimation of elk during population restoration to the Missouri Ozarks, USA. – Anim. Conserv. 26: 789–801.
Roberts, C. P., Cain, J. W. and Cox, R. D. 2017. Identifying ecologically relevant scales of habitat selection: diel habitat selection in elk. – Ecosphere 8: e02013.
Rumble, M. A. and Gamo, R. S. 2011. Resource selection by elk at two spatial scales in the Black Hills, South Dakota. – Prairie Nat. 43: 3–13.
Schneider, J., Maehr, D. S., Alexy, K. J., Cox, J. J., Larkin, J. L. and Reeder, B. C. 2006. Food habits of reintroduced elk in southeastern Kentucky. – Southeast. Nat. 5: 535–546.
Signer, J., Fieberg, J. and Avgar, T. 2019. Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. – Ecol. Evol. 9: 880–890.
Smith, B. D., Delgiudice, G. D. and Severud, W. J. 2021. Technological advances increase fix-success for white-tailed deer GPS collars. – Wildl. Soc. Bull. 45: 333–339.
Smith, T. N., Keller, B. J., Chitwood, M. C., Hansen, L. P. and Millspaugh, J. J. 2018. Diet composition and selection of recently reintroduced elk in Missouri. – Am. Midl. Nat. 180: 143–159.
Smith, T. N., Rota, C. T., Keller, B. J., Chitwood, M. C., Bonnot, T. W., Hansen, L. P. and Millspaugh, J. J. 2019. Resource selection of a recently translocated elk population in Missouri. – J. Wildl. Manage. 83: 365–378.
Tennessee Wildlife Resources Agency. 2018. Tennessee strategic elk management plan 2018–2027. – Tennessee Wildlife Resources Agency.
Therneau, T. 2024. A package for survival analysis in R. – R package ver. 3.7-0. CRAN: package survival (r-project.org). – https://cran.r-project.org/web/packages/survival/citation.html.
Thompson, I. D., Wiebe, P. A., Mallon, E., Rodgers, A. R., Fryxell, J. M., Baker, J. A. and Reid, D. 2015. Factors influencing the seasonal diet selection by woodland caribou (*Rangifer tarandus tarandus*) in boreal forests in Ontario. – Can. J. Zool. 93: 87–98.
Tomkiewicz, S. M., Fuller, M. R., Kie, J. G. and Bates, K. K. 2010. Global positioning system and associated technologies in animal behaviour and ecological research. – Phil. Trans. R. Soc. B 365: 2163–2176.
Verch, M. 2023. Fine-scale resource selection by elk (*Cervus canadensis*) in northcentral Pennsylvania. – MSc thesis, Indiana University of Pennsylvania, USA.
Verch, M. B., Padilla, B. J., Duchamp, J. E., Banfield, J. E. and Larkin, J. L. 2024. Data from: Seasonal fine-scale resource selection of elk in the central Appalachian Mountains. – Dryad Digital Repository, https://doi.org/10.5281/zenodo.13864406.