# Research Article



# Nutritional Carrying Capacity for Cervids Following Disturbance in Hardwood Forests

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ABSTRACT Closed-canopy forests dominate the landscape across much of the eastern United States and often lack a well-developed understory, which limits nutrition available for cervids. We evaluated the influence of timber harvest combined with prescribed fire, herbicide treatment, or fire and herbicide treatment in young mixed-hardwood forests on forage availability and nutritional carrying capacity (NCC) for elk (Cervus canadensis) and white-tailed deer (Odocoileus virginianus) in the Cumberland Mountains, Tennessee, USA, July-August 2013-2015. We compared forage availability, NCC using a 12% and 14% crude protein nutritional constraint, and vegetation composition in untreated mature forest stands, reclaimed surface mines, and 6 timber harvest treatments (timber harvest only, with early growing-season fire, with late growing-season fire, with herbicide only, with herbicide and early growing-season fire, and with herbicide and late growing-season fire). Forage availability in treatments involving timber harvest was greater than in untreated mature forest stands and reclaimed surface mines. Forage availability estimates in treatments involving herbicide and prescribed fire were less than all other timber harvest treatments. Nutritional carrying capacity estimates at the 12% and 14% crude protein constraints were greater in timber harvest treatments and on reclaimed surface mines than in untreated mature forest stands. Herbaceous species coverage was greater and woody species coverage was less on reclaimed surface mines and in timber harvest treatments involving herbicide and prescribed fire than in all other timber harvest treatments and untreated mature forest stands. Greater coverage of herbaceous forage species in treatments involving herbicide and prescribed fire and on reclaimed surface mines compensated for reduced forage availability and resulted in NCC estimates similar to all other timber harvest treatments. Our data indicate using periodic prescribed fire and following an herbicide application with prescribed fire are effective techniques to transition young mixed-hardwood forest communities to early successional communities and maintain increased forage availability and NCC for elk and deer. © 2018 The Wildlife Society.

KEY WORDS cervid, deer, elk, forage availability, herbicide, nutritional carrying capacity, prescribed fire, young forest.

An estimated 10,000,000 elk (*Cervus canadensis*) occupied North America prior to European settlement (Seton 1927). Elk populations subsequently declined and the species was extirpated throughout much of eastern North America owing to habitat loss and overexploitation (O'Gara and Dundas 2002). Several state wildlife agencies in the eastern United States, including those in Arkansas, Kentucky, Missouri, North Carolina, Pennsylvania, Tennessee, Virginia, and West Virginia, are working to restore elk populations in select areas. Elk are an important species ecologically, economically, and socially as they provide recreational opportunities for hunters, photographers, artists,

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and other wildlife enthusiasts (U.S. Fish and Wildlife Service [USFWS] 2011). Successful restoration of elk in the eastern United States hinges on the successful restoration and maintenance of elk habitat, which also could enhance habitat for white-tailed deer (Odocoileus virginianus). Closed-canopy mature forests currently dominate the landscape across much of the eastern United States and limit available sunlight to stimulate and support understory vegetation (Anderson and Katz 1993, Rossell et al. 2005, Webster et al. 2005, Shaw et al. 2010, McCord et al. 2014). Closed-canopy forests limit food and cover resources for many wildlife species that benefit from a well-developed forest understory or early successional vegetation communities, including elk and white-tailed deer (Beck and Harlow 1981, Johnson et al. 1995, Lashley et al. 2011, McCord et al. 2014, Cook et al. 2016). The prominence of closed-canopy forest in the eastern United States threatens the success of elk restoration

so techniques to increase nutritional carrying capacity should be evaluated if elk populations are expected to thrive in these areas.

Young forest stands (stand initiation stage) provide greater forage availability for elk and white-tailed deer than stands that have experienced canopy closure (stem exclusion stage and beyond; Ford et al. 1993, Strong and Gates 2006, Cook et al. 2016). Young forests provide large amounts of highly nutritious, digestible, and selected forage species for elk and white-tailed deer (Irwin and Peek 1983, Edge et al. 1988, Ford et al. 1993, Johnson et al. 1995). Nutritional demands of elk and white-tailed deer are greatest during summer to support lactation and juvenile growth (Oftedal 1985, Cook et al. 1996, Hewitt 2011). Inadequate summer forage availability results in poor nutrition, which may negatively affect pregnancy rates, age at first breeding, fetal survival, birth weight, juvenile growth, juvenile survival, and adult survival of elk (Cook et al. 1996, 2004; Hewitt 2011). Nutritional requirements and foraging preferences of elk and white-tailed deer are similar (Cook 2002, Beck and Peek 2005, Hewitt 2011), but their foraging strategies are different. Elk have greater digestive capabilities and a wider range of foraging options in comparison to white-tailed deer because elk are intermediate feeders, whereas white-tailed deer are concentrate selectors (Cook 2002, Hewitt 2011). which is the most limited of the morphophysiological feeding types (Hofmann 1988). Young forest stands in the eastern United States are dominated by woody species that provide browse, with lesser amounts of forbs that serve as the most-selected forage group by elk and white-tailed deer during summer (Waller and Alverson 1997, Beck and Peek 2005, Schneider et al. 2006, Lupardus et al. 2011). Increasing disturbance to set-back succession in mixed-hardwood forest stands is essential to provide high-quality forage plants, increase forage availability, and increase nutritional carrying capacity (NCC) for elk and white-tailed deer.

Disturbance techniques, such as canopy reduction, prescribed fire, and herbicide applications, may increase forage availability and improve forage quality for elk and whitetailed deer. Canopy reduction methods, such as clearcutting, shelterwood harvest, improvement cuts, and thinning operations, allow increased sunlight to the forest floor, which stimulates additional browse, and herbaceous forage (Collins and Urness 1983, Ford et al. 1993, Strong and Gates 2006, Lashley et al. 2011, Cook et al. 2016). Characteristics of closed-canopy forests in the eastern United States often make it necessary to couple canopy disturbance with prescribed fire to achieve increased forage for cervids (Masters et al. 1993, Sachro et al. 2005, Van Dyke and Darragh 2007, Shaw et al. 2010, Lashley et al. 2011). Varying seasonality (dormant, early growing season, and late growing season) and frequency of prescribed fire changes vegetation composition, which can affect forage quantity and quality for cervids (Gruchy et al. 2009, VanderYacht et al. 2017). The use of herbicides to manipulate vegetation composition and control undesirable plant species can increase the availability of more nutritious vegetation and has implications for increasing forage availability for elk and

white-tailed deer (Hurst and Warren 1986, Rice et al. 1997, Edwards et al. 2004, Chamberlain and Miller 2006).

Combining timber harvest, prescribed fire, and herbicide techniques to set-back succession and to improve and maintain forage availability and NCC for elk and deer in the eastern United States may be an efficient approach when working to restore elk habitat in areas where closed-canopy forests dominate the landscape and threaten the success of elk restoration. Early successional plant communities are an important component of elk and white-tailed deer habitat because they provide high-quality summer nutrition and cover. Understanding how to best transition closed-canopy forests to early successional communities is imperative for those working to restore habitat for elk in forest-dominated regions throughout the eastern United States. Our objectives were to evaluate the influence of timber harvest combined with prescribed fire, herbicide application, or fire and herbicide application in young mixed-hardwood forest stands on vegetation composition, forage availability, and NCC for elk and white-tailed deer. We hypothesized NCC for elk and deer would be most effectively increased and maintained in timber harvest treatments that involved repeated prescribed fire and that treatments involving herbicide application would reduce woody species composi-

# **STUDY AREA**

We conducted our research from July-August 2013-2015 across portions of the North Cumberland Wildlife Management Area (WMA), located in Anderson, Campbell, and Scott counties, Tennessee, USA. The North Cumberland WMA is central to the Tennessee Elk Restoration Zone and serves as the focus of elk management in Tennessee. The Tennessee Wildlife Resources Agency (TWRA) released 201 elk across the North Cumberland Wildlife WMA from 2000-2008 with the objective of reaching a population of 1,400-2,000 elk within 3 decades (TWRA 2016). Elevation (600-1,000 m), weather, and geographical characteristics were similar across all sites. In addition to the mountainous terrain, a history of strip, bench, and deep coal mining in the area resulted in benches and valleys distributed throughout the study area. Shale and siltstone influences have resulted in acidic, loamy, and well-drained soils (Conner 2002). Mean daily temperatures ranged from 1°C to 24°C and mean annual precipitation was 137 cm (National Oceanic and Atmospheric Administration 2016). The North Cumberland WMA is approximately 60,750 ha and is centrally located within Tennessee's 272,000-ha elk restoration zone. The dominant vegetation type across the study area was mixed-hardwood forest (87%) with interspersed openings characterized as reclaimed surface mines or wildlife openings (12%) and a small cropland component (1%; TWRA 2000). Mature forest across the study area primarily consisted of oak (Quercus spp.), hickory (Carya spp.), maple (Acer spp.), and yellow-poplar (Liriodendron tulipifera) with lesser amounts of American beech (Fagus grandifolia) and pine (Pinus spp.) interspersed. Reclaimed surface mines were dominated by tall fescue (Schedonorus arundinaceus) and sericea lespedeza

(Lespedeza cuneata) with scattered autumn olive (Eleagnus umbellata) and black locust (Robinia psuedoacacia). Most wildlife openings were mowed annually and dominated by perennial cool-season grasses (tall fescue, orchardgrass [Dactylis glomerata], and timothy [Phleum pretense]) with native forb species and perennial clovers present to a lesser extent.

# **METHODS**

#### Study Design

We selected 18 young forest stands across the North Cumberland WMA and separated them into 6 treatments. Each of the 18 young forest stands, ranging from 4 ha to 6 ha  $(\bar{x} = 5 \text{ ha})$ , were harvested in 2010. The 6 young forest treatments were timber harvest only (n = 3), timber harvest with early growing-season fire (n=4), timber harvest with late growing-season fire (n=2), timber harvest with herbicide only (n = 3), timber harvest with herbicide and early growing-season fire (n = 4), and timber harvest with herbicide and late growing-season fire (n = 2). Additionally, we selected portions of untreated mature forest stands (n=4) and reclaimed surface mines (n=3), ranging from 6 ha to 14 ha  $(\bar{x} = 10 \text{ ha})$ , to serve as controls because they were the mostprevalent vegetation types across the study area. Subsequently, we contracted a professional crew to treat timber harvest with herbicide only, timber harvest with herbicide and early growing-season fire, and timber harvest with herbicide and late growing-season fire stands with a foliar herbicide application consisting of a tank mixture of glyphosate (5%), imazapyr (1%), metsulfuron-methyl (0.15%), Optima® surfactant (0.10%), and Bullseye® spray pattern indicator (0.10%) in summer 2012. We used Accord® XRT II (glyphosate, 50.2%; Dow AgroSciences, Indianapolis, IN, USA) and DuPont® Lineage Clearstand (imazapyr, 63.2% and metsulfuron-methyl, 9.5%; DuPont, Wilmington, DE, USA) as mixing agents to achieve the appropriate tank mix ratio. Late growing-season fire treatments were applied to timber harvest with late growing-season fire stands and timber harvest with herbicide and late growing-season fire stands in fall 2012 and 2014 and early growing-season fire treatments were applied to timber harvest with early growing-season fire stands and timber harvest with herbicide and early growing-season fire stands in spring 2013 and 2015.

We assigned 190 random data collection points in treatment stands (≥5 points/stand depending on size), mature forest stands (10 points/stand), and mine sites (10 points/site) using ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA). We buffered the data collection points (≥40 m) from the stand boundaries to avoid the influence of edge effects on the plant community. We collected data to estimate vegetation composition, forage availability, browse selectivity, and NCC at each predetermined point during July–August 2013–2015.

# Response Variables

Vegetation composition.—We used the point-intercept transect method to collect vegetation composition data

(Canfield 1941). We established a 40-m line transect along the slope contour centered on each random point determined by ArcGIS. We recorded each plant species that intercepted each transect at 2-m intervals.

Forage availability.—We collected palatable biomass within 2 randomly placed  $1\text{-m}^2$  forage collection frames along each transect to gather data to estimate forage availability and forage quality. We considered leaf biomass and young twig ends ( $\leq 1$  growing season) from woody plants and herbaceous plants (excluding large stems) to be palatable and collected only those that were  $\leq 2$  m vertical height within the collection frame (Lashley et al. 2014). We bagged forages separately according to genus in forage collection bags and labeled each sample. We did not use data from our forage collection frames to calculate species composition.

We dried all forage samples to constant mass in an air-flow dryer at 50°C. We weighed dried forage samples using a digital scale and recorded weight in grams. We packaged and submitted forage samples from each genus within each treatment stand, untreated mature forest stand, and reclaimed surface mine for nutritional analysis (i.e., nitrogen, acid detergent fiber, neutral detergent fiber, phosphorus, potassium, calcium, magnesium, manganese, zinc, copper, iron, sulfur, sodium) using a wet chemistry nitrogen combustion technique at the Agricultural Service Laboratory at Clemson University (Clemson, SC, USA). The method of plant tissue analysis conducted by the staff in the laboratory required the following steps: re-dry each sample at 60°C, grind each sample in a Thomas Wiley mill to homogeneity, analytically weigh each ground sample into a foil, place the sample in foil in an autosampler carousel of Leco FP-528 Nitrogen Combustion Analyzer, combust sample in instrument following manufacturer's procedure, and determine percent nitrogen after combustion in the instrument taking beginning sample weight into consideration (Mills and Jones 1996, LECO Corporation 2000). Using wet chemistry is especially important when measuring nutritional content of naturally occurring forages because the most common alternative method, near infrared reflectance spectroscopy (NIRS), is based on reference evaluations of nutrients from calibrated forages analyzed by wet chemistry. The majority of forage species considered in this study have not had reference evaluations to develop calibrations for the NIRS method.

Browse selectivity.—We obtained browse selectivity data by recording evidence of browsing on individual plants detected along 40-m point-intercept transects at 2-m intervals. We documented browse intensity by comparing the number of stems eaten (use) to the number of stems available (availability) on each species detected at each point (Shaw et al. 2010). We used the browse intensity data to develop a use versus availability index to rank selected forages (Chesson 1983)

Nutritional carrying capacity.—We estimated NCC using a mixed-diet approach incorporating nutritional constraints as outlined in Hobbs and Swift (1985) to estimate white-tailed deer and elk days/ha as the metric of comparison for our results. Forage of low quality, relative to requirement, does not satisfy nutritional needs of cervids and other

ruminant herbivores, no matter the quantity. This concept is fundamental to the Hobbs and Swift (1985) algorithm and is important to our research because the nutritional quality of naturally occurring forages is widely variable. We included only forage species that were identified as selected species from our selectivity index or from related literature to reduce overestimation in the NCC model. We selected nutritional constraints based on crude protein requirements for antler growth (12%) and peak lactation (14%) for elk and whitetailed deer (Cook 2002, Hewitt 2011). We considered crude protein an appropriate metric to determine NCC during summer because of the large protein burden on females during lactation that must be met through their diet rather than body reserves (Sadleir 1987). Lactation also increases the digestible energy burden that may be a more limiting summer-autumn nutritional requirement for elk and other cervids, especially in regions where available forages are commonly high in tannins (Cook et al. 2004, 2016). However, condensed tannins have been reported to minimally affect the digestibility of selected cervid forages in the southeastern United States, so we elected to focus on crude protein (Jones et al. 2010, Lashley et al. 2015). We used the average lactation intake rates of a female elk weighing 236 kg (7.7 kg [dry mass]/day) and a white-tailed deer female weighing 50 kg (2.3 kg [dry mass]/day) to complete the NCC model (Cook 2002, Hewitt 2011).

## **Data Analysis**

Our experimental design was a completely randomized design with replication, sampling, and repeated measures. We conducted mixed-model analyses of variance using SAS 9.4 (SAS Institute, Cary, NC, USA) to compare means of forage availability, NCC, and vegetation composition among treatment stands and sampled vegetation types. We used the Tukey's procedure to compare means at  $\alpha=0.05$ . We gave unique subject numbers to each data collection point because we revisited the same points in each year of the study. Fixed effects were treatment, year, and treatment  $\times$  year. Random effects were replication within treatment and subject within replication. We developed orthogonal contrasts to gain greater insight to our data and explain differences between treatments when treatment  $\times$  year interactions were present. Using orthogonal contrasts enabled us to directly compare treatments

and combine treatments for comparison (i.e., all treatments involving herbicide, early and late growing-season fire treatments).

We developed a selection index to rank all detected forage species based on browse selectivity (Chesson 1983). We calculated an index value based on the number of stems of plant species that were browsed compared to the proportion of each species available. We considered species that ranked at or above the fifteenth percentile in the selectivity index to be moderately or highly selected.

# **RESULTS**

# **Vegetation Composition**

There was a treatment  $\times$  year interaction (P < 0.001) for woody species (shrubs, trees, and woody vines) coverage (Table 1). Orthogonal contrasts ( $\alpha = 0.05$ ) for all years indicated woody composition in timber harvest only (47  $\pm$  5 [SE]%, 37-57 [95% CI]) was greater than timber harvest with herbicide only treatments (32  $\pm$  5, 22–42), prescribed fire only treatments ( $29 \pm 5$ , 19-39), treatments involving herbicide and prescribed fire (15  $\pm$  6, 9–21), and reclaimed surface mines (15  $\pm$  5, 5–25) but similar to untreated mature forest stands ( $45 \pm 5$ , 35-55). Woody composition did not differ in timber harvest stands treated only with herbicide versus stands treated with prescribed fire alone, but combining herbicide with prescribed fire decreased woody composition more than using herbicide or prescribed fire alone. Woody composition was greater in timber harvest with herbicide only and prescribed fire only treatments than reclaimed surface mines. We did not detect a differences in woody composition between reclaimed surface mines and treatments that combined herbicide and prescribed fire. Woody species coverage was similar between early growingseason (31  $\pm$  5, 21-41) and late growing-season prescribed fire treatments  $(32 \pm 5, 22-42)$ .

There was a treatment  $\times$  year interaction for herbaceous species (forbs, grasses, sedges, rushes, ferns) coverage (Table 2). Orthogonal contrasts ( $\alpha=0.05$ ) for all years detected differences in herbaceous composition between untreated mature forest stands, reclaimed surface mines, and young forest treatments. Herbaceous species coverage was less in untreated mature forest stands ( $20\pm 8$ , 4–36) than in

Table 1. Coverage of woody species (%) by year and treatment at North Cumberland Wildlife Management Area, Tennessee, USA, July-August 2013–2015.

	Year <sup>a</sup>										
		201	3		201	4		20	15		
Treatment	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI		
Mature forest	51	±5	±10	48	±5	±10	37	±5	±10		
Timber harvest only	54	$\pm 5$	$\pm 10$	38	$\pm 5$	$\pm 10$	57	$\pm 5$	$\pm 10$		
Timber harvest with herbicide	39	$\pm 5$	$\pm 10$	30	$\pm 5$	$\pm 10$	35	$\pm 5$	$\pm 10$		
Timber harvest with early growing-season fire	32	$\pm 5$	$\pm 10$	35	$\pm 5$	$\pm 10$	25	$\pm 5$	$\pm 10$		
Timber harvest with late growing-season fire	37	$\pm 5$	$\pm 10$	32	$\pm 5$	$\pm 10$	26	$\pm 5$	$\pm 10$		
Timber harvest with herbicide and early growing-season fire	31	$\pm 5$	$\pm 10$	20	$\pm 5$	$\pm 10$	15	$\pm 5$	$\pm 10$		
Timber harvest with herbicide and late growing-season fire	17	$\pm 6$	$\pm 12$	15	$\pm 6$	$\pm 12$	9	$\pm 6$	$\pm 12$		
Reclaimed surface mine	17	$\pm 5$	$\pm 10$	20	$\pm 5$	$\pm 10$	13	$\pm 5$	$\pm 10$		

<sup>&</sup>lt;sup>a</sup>Treatment  $\times$  year effect significant ( $F_{14,325} = 4.16$ , P < 0.001).

Table 2. Coverage of herbaceous species (%) by year and treatment at North Cumberland Wildlife Management Area, Tennessee, USA, July-August 2013-2015.

	Year <sup>a</sup>										
				2013				15			
Treatment	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI		
Mature forest	21	±8	±16	23	±8	±16	15	±8	±16		
Timber harvest only	51	$\pm 9$	$\pm 18$	21	$\pm 9$	$\pm 18$	6	$\pm 9$	$\pm 18$		
Timber harvest with herbicide	61	$\pm 9$	$\pm 18$	43	$\pm 9$	$\pm 18$	24	$\pm 9$	$\pm 18$		
Timber harvest with early growing-season fire	75	$\pm 9$	$\pm 18$	30	$\pm 9$	$\pm 18$	22	$\pm 9$	$\pm 18$		
Timber harvest with late growing-season fire	50	$\pm 10$	$\pm 20$	25	$\pm 10$	$\pm 20$	29	$\pm 10$	$\pm 20$		
Timber harvest with herbicide and early growing-season fire	73	$\pm 10$	$\pm 20$	62	$\pm 10$	$\pm 20$	56	$\pm 10$	$\pm 20$		
Timber harvest with herbicide and late growing-season fire	77	$\pm 10$	$\pm 20$	61	$\pm 10$	$\pm 20$	73	$\pm 10$	$\pm 20$		
Reclaimed surface mine	69	$\pm 9$	$\pm 18$	70	$\pm 9$	$\pm 18$	68	$\pm 9$	$\pm 18$		

<sup>&</sup>lt;sup>a</sup> Treatment × year effect significant ( $F_{14,325} = 13.82$ , P < 0.001).

harvest treatments (47,  $\pm$ 12, 23–61) and on reclaimed surface mines (69  $\pm$ 9, 51–87). Reclaimed surface mines had similar proportions of herbaceous coverage to treatments involving herbicide and prescribed fire (67  $\pm$ 10, 47–87) but greater than timber harvest only (27  $\pm$ 9, 9–45), timber harvest and herbicide only (43  $\pm$ 9, 25–61), and prescribed fire only treatments (38  $\pm$ 9, 20–56). Herbaceous coverage increased when herbicide was combined with prescribed fire (67  $\pm$ 10, 47–87), as opposed to herbicide alone and prescribed fire only treatments. There was no difference in herbaceous species coverage between early growing-season (53  $\pm$ 10, 33–73) and late growing-season prescribed fire treatments (53  $\pm$ 11, 31–75).

There was a treatment  $\times$  year interaction for bramble species (blackberry [Rubus spp.], raspberry [Rubus spp.], greenbrier [Smilax spp.], and wild rose [Rosa spp.]) coverage (Table 3). Orthogonal contrasts ( $\alpha = 0.05$ ) for all years indicated untreated mature forest stands (7  $\pm$  4, 0–15) and reclaimed surface mines  $(6 \pm 5, 0-16)$  had less bramble coverage than young forest treatments (39  $\pm$  4, 31–47). Bramble coverage in treatments that included an herbicide application (29  $\pm$ 5, 19-39) was less than treatments without herbicide application (49  $\pm$  6, 37–61). Bramble coverage was reduced in treatments that incorporated fire with herbicide  $(26 \pm 6, 14-38)$ as opposed to using fire alone (49  $\pm$  5, 39–59). Bramble coverage in the timber harvest and herbicide only stands  $(34 \pm 6, 22-46)$ was similar to combined herbicide and fire treatments. Bramble coverage was similar among treatments involving early growing-season ( $36 \pm 6$ , 24–48) and late growing-season prescribed fire  $(40 \pm 6, 28-52)$ .

## Forage Availability

There was a treatment x year interaction within forage availability estimates (Table 4). Using orthogonal contrasts  $(\alpha = 0.05)$ , forage availability in untreated mature forest stands (147 kg/ha  $\pm$  27, 94–200) and on reclaimed surface mines  $(363 \pm 64, 238-488)$  did not differ and was less than all young forest treatments  $(1,124 \pm 100, 927-1,321)$  across all years. Forage availability in harvested stands that were not treated with fire, timber harvest only  $(1,116 \pm 98, 924-1310)$ and timber harvest with herbicide only  $(1,220 \pm 141,$ 1,079-1,361), were similar to stands that were burned  $(1,101 \pm 96, 913-1,289)$ . Forage availability decreased when herbicide was combined with prescribed fire  $(934 \pm 93,$ 751-1,117) in comparison to timber harvest treatments involving prescribed fire alone  $(1,270 \pm 98, 1,078-1,462)$ and herbicide alone but did not differ when compared to timber harvest only stands. Seasonality of fire did not result in differences between timber harvest with early growingseason fire  $(1,183 \pm 109, 970-1,396)$  and timber harvest with late growing-season fire  $(1,357 \pm 88, 1,185-1,529)$ treatments. Forage availability declined 5 years post-harvest in the timber harvest only treatment (778  $\pm$  73, 635–921) to a level approaching reclaimed surface mines and untreated mature forest stands.

#### **Browse Selectivity**

We detected 297 plant species using the point-intercept transect method during our study. Out of those 297 species, we identified 28 species as moderately or highly selected forages using a fifteenth percentile selection cut-off value

Table 3. Coverage of bramble species (%) by year and treatment at North Cumberland Wildlife Management Area, Tennessee, USA, July-August 2013–2015.

	Year <sup>a</sup>										
		201	3		201	4		20	15		
Treatment	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI		
Mature forest	9	±5	±10	7	±4	±8	3	±3	±6		
Timber harvest only	71	$\pm 7$	$\pm 14$	40	$\pm 6$	$\pm 12$	34	$\pm 4$	$\pm 8$		
Timber harvest with herbicide	37	$\pm 6$	$\pm 12$	25	$\pm 5$	$\pm 10$	39	$\pm 5$	$\pm 10$		
Timber harvest with early growing-season fire	53	$\pm 7$	$\pm 14$	35	$\pm 5$	$\pm 10$	47	$\pm 6$	$\pm 12$		
Timber harvest with late growing-season fire	74	$\pm 6$	$\pm 12$	43	$\pm 5$	$\pm 10$	44	$\pm 5$	$\pm 10$		
Timber harvest with herbicide and early growing-season fire	35	$\pm 5$	$\pm 10$	18	$\pm 5$	$\pm 10$	27	$\pm 6$	$\pm 12$		
Timber harvest with herbicide and late growing-season fire	35	$\pm 6$	$\pm 12$	24	$\pm 6$	$\pm 12$	19	$\pm 5$	$\pm 10$		
Reclaimed surface mine	7	$\pm 5$	$\pm 10$	8	$\pm 5$	$\pm 10$	6	$\pm 5$	$\pm 10$		

<sup>&</sup>lt;sup>a</sup>Treatment × year effect significant ( $F_{14.359} = 8.90$ , P < 0.001).

Table 4. Total forage available (kg/ha) in timber harvest treatments, mature forest stands, and reclaimed mine sites at North Cumberland Wildlife Management Area, Tennessee, USA, July-August, 2013–2015.

	Year <sup>a</sup>										
		2013			2014			2015			
Treatment	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI		
Mature forest	141	±17	±33	124	±20	±39	176	±44	±86		
Timber harvest only	1,160	$\pm 106$	$\pm 208$	1,411	$\pm 115$	$\pm 225$	778	$\pm 73$	$\pm 143$		
Timber harvest with herbicide	1,158	$\pm 136$	$\pm 267$	1,056	$\pm 104$	$\pm 204$	1,446	$\pm 124$	$\pm 243$		
Timber harvest with early growing-season fire	972	$\pm 118$	$\pm 231$	1,316	$\pm 98$	$\pm 100$	1,261	$\pm 110$	$\pm 215$		
Timber harvest with late growing-season fire	1,168	$\pm 86$	$\pm 167$	1,479	$\pm 86$	$\pm 169$	1,423	$\pm 91$	$\pm 178$		
Timber harvest with herbicide and early growing-season fire	753	$\pm 101$	$\pm 198$	937	$\pm 85$	$\pm 167$	1,050	$\pm 120$	$\pm 24$		
Timber harvest with herbicide and late growing-season fire	761	$\pm 61$	$\pm 120$	1,031	$\pm 91$	$\pm 93$	1,071	$\pm 101$	$\pm 198$		
Reclaimed surface mine	363	$\pm 73$	$\pm 143$	348	$\pm 50$	$\pm 98$	378	$\pm 68$	$\pm 133$		

<sup>&</sup>lt;sup>a</sup> Treatment × year effect significant ( $F_{7,13} = 19.83$ , P < 0.001).

(Table 5). Almost half of the selected forage species were forbs (13 species), whereas 2 bramble species, 3 vine species, 5 shrub species, and 5 tree species were selected. Although we detected 21 graminoid species, no grasses were selected by elk or white-tailed deer.

# **Nutritional Carrying Capacity**

There was a treatment  $\times$  year interaction (P < 0.001) when we evaluated NCC at the 12% crude protein constraint (Table 6). Orthogonal contrasts identified differences ( $\alpha = 0.05$ ) in NCC between treatments at the 12% crude protein constraint across all years. Nutritional carrying capacity was greater in all timber harvest treatments in

comparison to untreated mature forest stands. Nutritional carrying capacity on reclaimed surface mines was similar to timber harvest only, timber harvest with herbicide only, and combined herbicide and fire treatments, but NCC was less on reclaimed surface mines than in fire only treatments. Following timber harvest with herbicide, prescribed fire, or a combination of herbicide and prescribed fire did not increase or decrease NCC at the 12% crude protein constraint. Seasonality of fire had no impact on NCC.

There was a treatment effect (P=0.001) when we estimated NCC at the 14% crude protein nutritional constraint (Table 7). Nutritional carrying capacity in untreated mature forest stands was less than all timber

Table 5. Selected forages as determined by selection transects at North Cumberland Wildlife Management Area, Tennessee, USA, July-August 2013-2015.

Common name Species		Life forma	Crude protein (%)			
Wild lettuce	Lactuca spp.	F	17.56			
Common greenbrier	Smilax rotundifolia	V	11.56			
Wood nettle	Laportea canadensis	F	12.35			
Jewelweed	Impatiens spp.	F	27.38			
Oldfield aster	Symphyotrichum pilosum	F	14.87			
White wood aster	Eurybia divaricata	F	16.25			
American pokeweed	Phytolacca americana	F	28.13			
Cankerweed	Prenanthes spp.	F	14.12			
Buffalo nut	Pyrularia pubera	S	19.38			
Queen Anne's lace	Daucus carota	F	17.06			
Striped maple	Acer pennsylvanicum	T	12.81			
Common ragweed	Ambrosia artemisiifolia	F	21.12			
Maple-leaf viburnum	Viburnum acerifolium	S	8.75			
Giant ragweed	Ambrosia trifida	F	17.81			
Joe-pye weed	Eupatorium purpureum	F	18.13			
Cat greenbrier	Smilax glauca	V	12.38			
Wild hydrangea	Hydrangea arborescens	S	14.18			
Woodland sunflower	Helianthes divaricatus	F	16.68			
Lowbush blueberry	Vaccinium angustifolium	S	9.61			
Blackgum	Nyssa sylvatica	T	12.68			
Canada goldenrod	Solidago canadensis	F	16.31			
Blackberry	Rubus argutus	В	11.88			
Black raspberry	Rubus occidentalis	В	12.56			
Smooth sumac	Rhus glabra	S	11.88			
Black birch	Betula nigra	T	12.31			
Grape	Vitis spp.	V	14.93			
Sourwood	Oxydendrum arboreum	T	13.38			
Red maple	Acer rubrum	T	11.31			

<sup>&</sup>lt;sup>a</sup> B, bramble; F, forb; S, shrub; T, tree; V, vine.

Table 6. Nutritional carrying capacity (animal days/ha) for elk and white-tailed deer at a 12% crude protein constraint at North Cumberland Wildlife Management Area, Tennessee, USA, July-August 2013–2015.

					Yea	r <sup>a</sup>			
		2013	3		2014	1		201	.5
Treatment	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI
Elk									
Mature forest	7	$\pm 2$	$\pm 4$	8	$\pm 2$	$\pm 4$	9	$\pm 3$	$\pm 6$
Timber harvest only	46	$\pm 8$	$\pm 16$	39	$\pm 10$	$\pm 20$	35	$\pm 8$	$\pm 16$
Timber harvest with herbicide	23	$\pm 3$	$\pm 6$	39	$\pm 8$	$\pm 16$	68	$\pm 10$	$\pm 20$
Timber harvest with early growing-season fire	45	$\pm 5$	$\pm 10$	61	$\pm 9$	$\pm 18$	49	$\pm 6$	$\pm 18$
Timber harvest with late growing-season fire	31	$\pm 4$	$\pm 8$	42	$\pm 6$	$\pm 12$	64	$\pm 9$	$\pm 18$
Timber harvest with herbicide and early growing-season fire	30	$\pm 3$	$\pm 6$	29	$\pm 4$	$\pm 8$	52	$\pm 10$	$\pm 20$
Timber harvest with herbicide and late growing-season fire	34	$\pm 3$	$\pm 6$	25	$\pm 3$	$\pm 6$	47	$\pm 6$	$\pm 12$
Reclaimed surface mine	31	$\pm 6$	$\pm 12$	27	$\pm 5$	$\pm 10$	35	$\pm 9$	$\pm 18$
White-tailed deer									
Mature forest	23	$\pm 5$	$\pm 10$	26	$\pm 7$	$\pm 14$	31	$\pm 10$	$\pm 20$
Timber harvest only	150	$\pm 27$	$\pm 53$	130	$\pm 34$	$\pm 67$	116	$\pm 25$	$\pm 49$
Timber harvest with herbicide	75	$\pm 11$	$\pm 22$	129	$\pm 25$	$\pm 49$	224	$\pm 33$	$\pm 65$
Timber harvest with early growing-season fire	149	$\pm 18$	$\pm 35$	202	$\pm 28$	$\pm 55$	163	$\pm 20$	±39
Timber harvest with late growing-season fire	102	$\pm 12$	$\pm 24$	139	$\pm 19$	$\pm 37$	212	$\pm 28$	$\pm 55$
Timber harvest with herbicide and early growing-season fire	100	$\pm 11$	$\pm 22$	95	$\pm 12$	$\pm 24$	171	$\pm 33$	$\pm 65$
Timber harvest with herbicide and late growing-season fire	111	$\pm 10$	$\pm 20$	82	$\pm 11$	$\pm 22$	155	$\pm 20$	$\pm 39$
Reclaimed surface mine	102	$\pm 20$	$\pm 39$	89	$\pm 16$	$\pm 31$	114	$\pm 30$	$\pm 59$

<sup>&</sup>lt;sup>a</sup> Treatment × year effect significant (F<sub>14,324</sub> = 4.68, P < 0.001). We analyzed nutritional carrying capacity for elk and deer separately.

harvest treatments and reclaimed surface mines. Nutritional carrying capacity was greater in timber harvest with early growing-season fire and timber harvest with late growing-season fire than timber harvest only and timber harvest with herbicide only. Nutritional carrying capacity estimates on reclaimed surface mines and in treatments that combined herbicide and fire were similar to all other timber harvest treatments.

## DISCUSSION

All timber harvest treatments increased forage availability and NCC in comparison to mature forest at North Cumberland WMA. However, periodic applications of prescribed fire were necessary to maintain increased forage availability and NCC following timber harvest. Combining herbicide and prescribed fire effectively maintained increased forage availability and NCC for elk and white-tailed deer and encouraged the transformation of young forest stands to early successional plant communities, which is critical to improve habitat for elk and white-tailed deer in primarily forested regions. We did not detect differences in vegetation

composition, forage availability, or NCC between early growing-season and late growing-season prescribed fire treatments. However, we collected data after only 2 burns and differences may emerge following continued applications of the prescribed fire treatments.

Forage availability in timber harvest treatments increased up to tenfold in comparison to mature forest stands. Studies in similar regions of the southern Appalachians also reported increases in forage availability and NCC for white-tailed deer following canopy disturbance (Beck and Harlow 1981, Ford et al. 1993, Lashley et al. 2011). Researchers in western forest systems have reported similar increases in summer forage availability and NCC for elk following timber harvest (Hett et al. 1978, Collins and Urness 1983, Strong and Gates 2006). However, forage availability and NCC benefits realized from timber harvest are short lived in the eastern United States because of rapid rates of forest regeneration and canopy closure.

Forage availability decreased 5 years following complete canopy removal without additional disturbance at North Cumberland WMA. Previous research has reported forage

Table 7. Nutritional carrying capacity for elk and deer (animal days/ha) at a 14% crude protein constraint at North Cumberland Wildlife Management Area, Tennessee, USA, July-August 2013–2015.

Treatment <sup>a</sup>		Elk		White-tailed deer				
	$\bar{x}$	SE	95% CI	$\bar{x}$	SE	95% CI		
Mature forest	7	±3	±6	22	±10	±20		
Timber harvest only	18	$\pm 4$	±8	60	$\pm 13$	±25		
Timber harvest with herbicide	20	$\pm 4$	±8	64	$\pm 13$	±25		
Timber harvest with early growing-season fire	32	$\pm 4$	±8	105	$\pm 13$	±25		
Timber harvest with late growing-season fire	31	$\pm 4$	±8	104	$\pm 15$	±29		
Timber harvest with herbicide and early growing-season fire	30	$\pm 4$	±8	97	$\pm 12$	$\pm 24$		
Timber harvest with herbicide and late growing-season fire	28	±5	$\pm 10$	91	$\pm 16$	±31		
Reclaimed surface mine	26	$\pm 4$	$\pm 8$	85	$\pm 12$	$\pm 24$		

<sup>&</sup>lt;sup>a</sup> Treatment effect significant ( $F_{7,17}$  = 5.93, P = 0.001). We analyzed nutritional carrying capacity for elk and white-tailed deer separately.

availability in young hardwood forest stands decreases to levels similar to mature forest stands 6–8 years after canopy removal as hardwood regeneration advances to a point of canopy closure and reduces available sunlight to the understory (Lashley et al. 2011, McCord et al. 2014).

Prescribed fire is an effective and cost efficient method of disturbance to increase the quality and quantity of forage for elk and white-tailed deer when adequate sunlight is available (Masters et al. 1993, Sachro et al. 2005, Van Dyke and Darragh 2007, Shaw et al. 2010, Lashley et al. 2011). Our data indicate a 5-year fire-return interval would maintain increased forage availability and NCC following timber harvest. More frequent fire-return intervals of 2–3 years may maintain higher-quality forage but require more intensive management.

Increasing the presence of early successional plant communities has major implications for improving forage availability and NCC for elk and white-tailed deer in areas where closed-canopy forests dominate the landscape. Forbs remain the most selected, most easily digested, and most nutritious summer forages for both ungulates, though elk are more digestively adaptive (Cook 2002, Hewitt 2011). Recent diet studies in Kentucky and Tennessee have detected high proportions of forbs in elk diets (Schneider et al. 2006, Lupardus et al. 2011). Using an herbicide application specifically designed to target woody sprouts reduced woody composition at North Cumberland WMA. The reduction in woody composition followed with prescribed fire encouraged greater herbaceous coverage in comparison to all other treatments and maintained increased NCC for elk and white-tailed deer. Additionally, a reduction in bramble composition occurred in stands that were treated with herbicide, which further reduced competition with herbaceous species. Using a combination of triclopyr herbicide and prescribed fire following retention cuts and shelterwood harvests did not increase forage availability or NCC for white-tailed deer or reduce woody species in comparison to using fire alone in east Tennessee (Lashley et al. 2011). The lack of woody control resulted from the establishment of hardwood seedlings that were not affected by the broadcast application of triclopyr, which has no residual soil activity and is safe for use under hardwoods (Dow AgroSciences 2005). Our treatments involved complete overstory removal, so we were not concerned about overstory tree mortality and could incorporate imazapyr into our herbicide application, which is not recommended for use when managing hardwood stands because of soil activity (BASF 2007). Our data suggest a growing-season application of 5% glyphosate, 1% imazapyr, and 0.15% metsulfuron-methyl in recently harvested mixed hardwood stands followed by periodic growing-season prescribed fire is effective in decreasing woody and bramble composition, increasing herbaceous composition, and encouraging growth of highquality forages for elk and deer.

It is important to understand that NCC estimates produced by the Hobbs and Swift (1985) algorithm and other NCC estimation techniques are almost always inflated in comparison to the true NCC of plant communities. Estimating NCC is a valuable technique used to compare available nutrition among different plant communities, but NCC results should always be interpreted as relative indices rather than exact estimates. Our decision to use crude protein as the model constraint created an assumption within the model that the only difference between forage species, in terms of their nutritional value to cervids, was crude protein. Digestible energy and digestible protein are generally considered to be the most relevant measurements of nutritional quality in forages for cervids, especially in arid (Meyer et al. 1984) and boreal (Parker et al. 1999) environments where digestible energy is often a limiting factor and condensed tannins greatly reduce digestibility (Hanley et al. 2012). However, negative impacts of condensed tannins on digestibility along with the availability of digestible energy are unlikely to be limiting factors for cervids in the subtropical environment of the southeastern United States (Jones et al. 2010, Lashley et al. 2015).

Prescribed fire is an irreplaceable tool in the restoration and maintenance of early successional plant communities, especially in rugged terrain where mechanical treatment is problematic or not possible. However, vegetation response to growing-season prescribed fire in hardwood-dominated regions of the central and eastern United States is not well-understood (Harper et al. 2016). Research has indicated burning during the dormant season or the early growing season only topkills young woody plants (Glitzenstein et al. 2012, McCord et al. 2014). Woody stem densities commonly increase following dormant-season prescribed fire and have been reported to remain the same or increase following early growing-season prescribed fire (Sparks et al. 1999, Drewa et al. 2002, Robertson and Hmielowski 2014). Fewer studies have evaluated the effects of late growing-season fire on young woody plants in hardwood regions. Applications of prescribed fire in June and August in the Ozark Mountains decreased hardwood sprouts in comparison to April burning (Lewis et al. 1964). In west Tennessee, late growing-season fire reduced woody encroachment and maintained an herbaceous-dominated plant community much more effectively than dormant-season fire (Gruchy et al. 2009). We did not detect differences in vegetation composition, forage availability, or NCC in response to seasonality of prescribed fire, but both prescribed fire treatments effectively decreased woody composition in comparison to timber harvest alone. Differences in woody composition related to seasonality of prescribed fire may be detected following additional prescribed fire treatments. Future research devoted to better understanding the relationships between vegetation composition and seasonality of fire would provide valuable information to managers and biologists who are working to restore and maintain early successional plant communities in hardwood-dominated regions of the eastern United States.

## MANAGEMENT IMPLICATIONS

Full canopy removal followed by periodic prescribed fire or an initial herbicide application followed with periodic prescribed fire will improve and maintain forage availability

and NCC for elk and white-tailed deer in forested landscapes in the eastern United States. Recurring prescribed fire will be required to maintain increased forage availability and NCC. Fire-return intervals should be determined by vegetation response and may vary year to year and across sites. However, it is clear from our data and other research that a fire-return interval within 5–8 years will be necessary to prevent canopy closure and maintain increased forage availability in mixed hardwood systems of the eastern United States. If the objective is to convert mixed-hardwood forest stands to early successional plant communities to maximize forage quality for elk and white-tailed deer, we recommend a targeted herbicide application in recently harvested stands (2-3 yrs post-harvest) to reduce coppice growth and young woody plants followed by prescribed fire on a 2-3-year return interval. The combination of this herbicide application with frequent applications of prescribed fire will reduce woody competition with herbaceous plants and accelerate the transition of young mixed-hardwood forest stands to early successional plant communities, which will be required to restore or maintain high-quality summer forage for elk and white-tailed deer on many sites in the eastern United States.

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# LITERATURE CITED

- Anderson, R. C., and A. J. Katz. 1993. Recovery of browse-sensitive tree species following release from whitetail deer *Odocoileus virginianus* Zimmerman browsing pressure. Biological Conservation 63:203–208.
- BASF Corporation. 2007. Arsenal AC label. BASF Agricultural Products, Research Triangle Park, North Carolina, USA.
- Beck, D. E., and R. F. Harlow. 1981. Understory forage production following thinning in Southern Appalachian cove hardwoods. Proceedings Annual Conference Southeastern Association of Fish and Wildlife Agencies 35:185–196.
- Beck, J. L., and J. M. Peek. 2005. Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. Rangeland Ecology and Management 58: 135–147.
- Canfield, R. H. 1941. Application of the line interception method in sampling range vegetation. Journal of Forestry 39:388–394.
- Chamberlain, M. J., and D. A. Miller. 2006. Effects of two site preparation techniques on biomass of forage plants for white-tailed deer in eastern Louisiana. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 60:64–69.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297–1304.
- Conner, C. T. 2002. Soil survey of Campbell County, Tennessee. United States Department of Agriculture, Natural Resources Conservation Service, Lincoln, Nebraska, USA.
- Cook, J. G., L. J. Quinlan, L. L. Irwin, L. D. Bryant, R. A. Riggs, and J. W. Thomas. 1996. Nutrition-growth relations of elk calves during summer and fall. Journal of Wildlife Management 60:528–541.
- Cook, J. G. 2002. Nutrition and food. Pages 259–349 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.

- Cook, J. G., B. K. Johnson, R. C. Cook, R. A. Riggs, T. Delcurto, L. D. Bryant., and L. L. Irwin. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs 155:1–61.
- Cook, J. G., R. C. Cook, R. W. Davis, and L. L. Irwin. 2016. Nutritional ecology of elk during summer and autumn in the Pacific Northwest. Wildlife Monographs 195:1–81.
- Collins, W. B., and P. J. Urness. 1983. Feeding behavior and habitat selection of mule deer and elk on northern Utah summer ranges. Journal of Wildlife Management 47:646–663.
- Dow AgroSciences. 2005. Garlon1 3-A herbicide label. DowAgroSciences LLC, Indianapolis, Indiana, USA.
- Drewa, P. B., W. J. Platt, and E. B. Moser. 2002. Fire effects on resprouting of shrubs in headwaters of southeastern longleaf pine savannas. Ecology 83:755–767.
- Edge, W. D., C. L. Marcum, and S. L. Olson-Edge. 1988. Summer forage and feeding site selection by elk. Journal of Wildlife Management 52: 573–577.
- Edwards, S. L., S. Demarais, B. Watkins, and B. K. Strickland. 2004. White-tailed deer forage production in managed and unmanaged pine stands and summer food plots in Mississippi. Wildlife Society Bulletin 32:739–745.
- Ford, W. M., A. Johnson, P. E. Hale, and J. M. Wentworth. 1993. Availability and use of spring and summer woody browse by deer in clearcut and uncut forests of the southern Appalachians. Southern Journal of Applied Forestry 17:116–119.
- Glitzenstein, J. S., D. R. Streng, R. E. Masters, K. M. Robertson, and S. M. Hermann. 2012. Fire-frequency effects on vegetation in north Florida pinelands: another look at the long-term Stoddard Fire Research Plots at Tall Timbers Research Station. Forest Ecology and Management 264: 197–209.
- Gruchy, J. P., C. A. Harper, and M. J. Gray. 2009. Methods for controlling woody invasion into CRP fields in Tennessee. Pages 315–321 in S. B. Cederbaum, B. C. Faircloth, T. M. Terhune, J. J. Thompson, J. P. Carroll, editors. Gamebird 2006: Quail VI and Perdix XII. Warnell School of Forestry and Natural Resources, Athens, Georgia, USA.
- Hanley, T. A., D. E. Spalinger, K. J. Mock, O. L. Weaver, and G. M. Harris. 2012. Forage resource evaluation system for habitat—deer: an interactive deer habitat model. U.S. Forest Service General Technical Report PNW-GRR-858, Washington, D.C., USA.
- Harper, C. A., W. M. Ford, M. A. Lashley, C. E. Moorman, and M. C. Stambaugh. 2016. Fire effects on wildlife in the Central Hardwoods and Appalachian regions. Fire Ecology 12:127–159.
- Hett, J., R. Taber, J. Long, and J. Schoen. 1978. Forest management policies and elk summer carrying capacity in the *Abies amabilis* forest, western Washington. Environmental Management 2:561–566.
- Hewitt, D. G. 2011. Biology and management of white-tailed deer. CRC Press, Boca Raton, Florida, USA.
- Hobbs, N. T., and D. M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. Journal of Wildlife Management 49:814–822.
- Hofmann, R. R. 1988. Anatomy of the gastro-intestinal tract. Pages 14–43 in D. D. Church, editor. The ruminant animal: digestive physiology and nutrition. Prentice Hall, Englewood Cliffs, New Jersey, USA.
- Hurst, G. A., and R. C. Warren. 1986. Deer forage on pine plantations after a herbicide application for pine release. Proceedings of the Southern Weed Science Society 39:238.
- Irwin, L. L., and J. M. Peek. 1983. Elk habitat use relative to forest succession in Idaho. Journal of Wildlife Management 47:664–672.
- Johnson, A. S., P. E. Hale, W. M. Ford, J. M. Wentworth, J. R. French, O. F. Anderson, and G. B. Pullen. 1995. White-tailed deer foraging in relation to successional stage, overstory type, and management of southern Appalachian forests. American Midland Naturalist 133:18–35.
- Jones, P. D., B. Rude, J. P. Muir, S. Demarais, B. K. Strickland, and S. L. Edwards. 2010. Condensed tannins' effect on white-tailed deer forage digestibility in Mississippi. Journal of Wildlife Management 74:707–713.
- Lashley, M. L., C. A. Harper, G. E. Bates, and P. D. Keyser. 2011. Forage availability for white- tailed deer following silvicultural treatments in hardwood forests. Journal of Wildlife Management 75:1467–1476.
- Lashley, M. A., M. C. Chitwood, C. A. Harper, C. E. Moorman, and C. S. DePerno. 2014. Collection, handling and analysis of forages for concentrate selectors. Wildlife Biology in Practice 10:29–38.

- Lashley, M. A., M. C. Chitwood, C. A. Harper, C. M. Moorman, and C. S. DePerno. 2015. Poor soils and density-mediated body weight in deer: forage quality or quantity? Wildlife Biology 21:213–219.
- LECO Corporation. 2000. FP-528 instruction manual. LECO Corporation, St. Joseph, Michigan, USA.
- Lewis, J. B., D. A. Murphy, and J. Ehrenreich. 1964. Effects of burning dates on vegetative production on Ozark forests. Pages 63–72 in Proceedings of the 18th Annual Conference of the Southeastern Association of Game and Fish Commissioners, Clearwater, Florida, USA.
- Lupardus, J. L., L. I. Muller, and J. L. Kindall. 2011. Seasonal forage availability and diet for reintroduced elk in the Cumberland Mountains, Tennessee. Southeastern Naturalist 10:53–74.
- Masters, R. E., R. L. Lochmiller, and D. M. Engle. 1993. Effects of timber harvest and prescribed fire on white-tailed deer forage production. Wildlife Society Bulletin 21:401–411.
- McCord, J. M., C. A. Harper, and C. H. Greenburg. 2014. Brood cover and food resources for wild turkeys following silvicultural treatments in mature upland hardwoods. Wildlife Society Bulletin 38:265–272.
- Meyer, M. W., R. D. Brown, and M. W. Graham. 1984. Protein and energy content of white-tailed deer diets in the Texas coastal bend. Journal of Wildlife Management 48:527–534.
- Mills, H. A., and J. B. Jones. 1996. Plant analysis handbook II: a practical sampling, preparation, analysis, and interpretation guide. Micromacro Publishing, Athens, Georgia, USA.
- National Oceanic and Atmospheric Administration. 2016. Climatological data annual summary Tennessee. National Climatic Data Center, Asheville, North Carolina, USA.
- Oftedal, O. T. 1985. Pregnancy and lactation. Pages 215–238 in R. J. Hudson and R. G. White, editors. Bioenergetics of wild herbivores. CRC Press, Boca Raton, Florida, USA
- O'Gara, B. W., and R. G. Dundas. 2002. Distribution: past and present. Pages 67–119 in D. E. Toweill and J. W. Thomas, editors. North American elk: ecology and management. Smithsonian Institution Press, Washington, D.C., USA.
- Parker, K. L., M. P. Gillingham, T. A. Hanley, and C. T. Robbins. 1999. Energy and protein balance of free-ranging black-tailed deer in a natural forest environment. Wildlife Monographs 143:3–48.
- Rice, P. M., J. C. Toney, D. Bedunah, and C. E. Carlson. 1997. Elk winter forage enhancement by herbicide control of spotted knapweed. Wildlife Society Bulletin 25:627–633.
- Robertson, K. M., and T. L. Hmielowski. 2014. Effects of fire frequency and season on resprouting of woody plants in southeastern US pine-grassland communities. Oecologia 174:765–776.
- Rossell, C. R., Jr., B. Gorsira, and S. Patch. 2005. Effects of white-tailed deer on vegetation structure and woody seedling composition in three forest types on the Piedmont Plateau. Forest Ecology and Management 210:415–424.
- Sachro, L. L., W. L. Strong, and C. C. Gates. 2005. Prescribed burning effects on summer elk forage availability in the subalpine zone, Banff

- National Park, Canada. Journal of Environmental Management 77: 183-193.
- Sadleir, R. M. F. S. 1987. Reproduction of female cervids. Pages 123–144 in C. M. Wemmer, editor. Biology and management of the Cervidae. Research Symposium of the National Zoological Park, Smithsonian Institution, Washington, D.C., USA.
- Seton, E. T. 1927. Lives of game animals. Volume. 3, part 1. Doubleday, Doran, and Company, Garden City, New York, USA.
- Schneider, J., D. S. Maehr, K. J. Alexy, J. J. Cox, J. L. Larkin, and B. C. Reeder. 2006. Food habits of reintroduced elk in southeastern Kentucky. Southeastern Naturalist 5:535–546.
- Shaw, C. E., C. A. Harper, M. W. Black, and A. E. Houston. 2010. The effects of prescribed burning and understory fertilization on browse production in closed-canopy hardwood stands. Journal of Fish and Wildlife Management 1:64–72.
- Sparks, J. C., R. E. Masters, D. M.Engle, M. E. Payton, and G. A. Bukenhofer 1999. Influence of fire season and fire behavior on woody plants in red-cockaded woodpecker clusters. Wildlife Society Bulletin 27: 124–133
- Strong, W. L., and C. C. Gates. 2006. Herbicide-induced changes to ungulate forage habitat in western Alberta, Canada. Forest Ecology and Management 222:469–475.
- Tennessee Wildlife Resources Agency. 2000. Proposal: elk restoration in the northern Cumberland Plateau, Tennessee. Tennessee Wildlife Resources Agency, Nashville, USA.
- Tennessee Wildlife Resources Agency [TWRA]. 2016. Elk reintroduction questions and answers. <a href="https://www.tn.gov/twra/article/elk-reintroduction-questions-answers">https://www.tn.gov/twra/article/elk-reintroduction-questions-answers</a>. Accessed 5 Jul 2017.
- U.S. Fish and Wildlife Service [USFWS]. 2011. National survey of fishing hunting, and wildlife-associated recreation. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Van Dyke, F., and J. A. Darragh. 2007. Response of elk to changes in plant production and nutrition following prescribed burning. Journal of Wildlife Management 71:23–29.
- Vander Yacht, A. L., S. A. Barrioz, P. D. Keyser, C. A. Harper, D. S. Buckley, D. A. Buehler, and R. D. Applegate. 2017. Vegetation response to canopy disturbance and season of burn during oak woodland and savanna restoration in Tennessee. Forest Ecology and Management 390: 187–202
- Waller, D. M., and W. S. Alverson. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:217–226.
- Webster, C. R., M. A. Jenkins, and J. H. Rock. 2005. Long-term response of spring flora to chronic herbivory and deer exclusion in Great Smoky Mountains National Park, USA. Biological Conservation 125:297–307.

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