



Original Article

Regaining the History of Deer Populations and Densities in the Southeastern United States

BRICE B. HANBERRY,¹ *USDA Forest Service, Rocky Mountain Research Station, 8221 Mt. Rushmore Rd., Rapid City, SD 57702, USA*

PHILLIP HANBERRY, *Missouri Resource Assessment Partnership (MoRAP), University of Missouri, Columbia, MO 65201, USA*

ABSTRACT Despite widespread interest in white-tailed deer (*Odocoileus virginianus*) in the southeastern United States, historical deer populations and densities have not been compiled into one accessible source. We digitized maps from 1950, 1970, 1982, and 2003 and reviewed literature to quantify population sizes and densities in the Southeast, although previous estimates may not be accurate. Deer population sizes declined to a minimum of <215,000 during the early 1900s. Population sizes and mean deer densities were 304,000 and 0.22 deer/km² by 1940, 476,000 and 0.35 deer/km² by 1950, 2.9 million to 4.1 million and 2.2 to 3.1 deer/km² by approximately 1970, 6.2 million and 4.6 deer/km² by 1982, and 10.8 million to 12 million and 8 to 9 deer/km² by about 2003. Although our estimates are likely not completely accurate in space and time, due to difficulty of counting animals, they provide the best available information and a range and trend in values, with general corroboration among sources. The current population size may be greater than during pre-Euro-American settlement, when based on minimum historical deer densities, or, conversely, the current population may be within the bounds of mid to high historical deer densities. Large deer densities trigger a research need to evaluate deer effects on vegetation, but threshold densities when deer are damaging to herbaceous plants may need to be reconsidered. Instead, we conjecture that deer may be considered a natural disturbance helpful in controlling increased tree densities during the past century, albeit placing a secondary stress upon declining herbaceous plants, which are losing ground to trees. © 2020 The Wildlife Society.

KEY WORDS archive, driver, eCognition, GIS, herbivory, *Odocoileus virginianus*, southeastern United States.

The presettlement population size of white-tailed deer (*Odocoileus virginianus*) in North America may have ranged anywhere from 24 million to 62 million, or even greater, based on potentially conservative deer density values of 3 to 8 deer per km² and a historical distribution of about 7.8 million km², of which 5.2 million km² was the range east of the Mississippi River (McCabe and McCabe 1984, Hanberry and Hanberry 2020). For minimum bounds, Adams and Hamilton (2011) calculated a population size of 9 million to 19 million animals before 1500 and subsequent introduction of novel diseases that reduced native American populations. The deer population size likely varied in time and space depending on factors such as available resources, weather (e.g., severe winters), climate (i.e., the Medieval Warm Period and Little Ice Age), densities of predators and humans, and disease. By 1800, deer populations may have decreased to about 12 to 14 million animals because deer supplied hides for trade with Europe and a

convenient food and fabric source for settling Euro-Americans (McCabe and McCabe 1984, Adams and Hamilton 2011). A stable or recovering deer population may have occurred for about 50 years, before exploitive hunting for markets during expansion westward in the United States between 1850 to 1900 reduced the deer population size to 300,000 to 500,000 animals (McCabe and McCabe 1984). Deer remained in areas that were remote and inaccessible to humans or protected by landowners. Although hunting restrictions were enacted as early as 1646, enforced protection by state and federal laws, such as the Lacey Act of 1900 that prevented interstate traffic in wild animals, ended market hunting during the early 1900s (McCabe and McCabe 1984).

The scarcity of deer probably reduced profitability of market hunting, which may have been the most effective deterrent to unrestrained harvest while supplies lasted, along with public support for sustainable deer management. Institution of state wildlife agencies with enforcement officers and establishment of public lands also contributed to deer recovery (Blackard 1971). By 1980, deer population size may have rebounded to 1850 values, of about 14 million animals, and by 2000, the deer population may have

Received: 26 January 2020; Accepted: 25 June 2020
Published: 27 August 2020

¹E-mail: brice.hanberry@usda.gov

returned to 30 million animals in the United States (McCabe and McCabe 1984, Webb 2014).

In the southeastern United States, unregulated hunting ended about 1920 when deer numbers for the region reached a record low, although the year of least deer populations varied by individual state (Newsom 1969, Blackard 1971). Events such as Mississippi River floods, diseases and culling to prevent spread of diseases, and deer harvest during World War II rationing placed stress on recovery of small, isolated deer populations (Newsom 1969). The 1940s population size was approximately 304,000 animals in 11 states: Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, the Carolinas, Tennessee, and Virginia, USA (Newsom 1969). Reintroduction of deer was an active process, perhaps initiated by private landowners during the early 1900s. However, by about 1950, every state had a deer restocking program, typically funded by provisions of the Pittman-Robertson Act of 1936 (Newsom 1969, Blackard 1971). Most deer were trapped and relocated within the southeastern states, although at least 6,000 deer were relocated from other sources, primarily Wisconsin and Texas, USA (Blackard 1971). By 1970, about 32,000 deer had been stocked into protected areas where deer were extirpated and population size had increased to about 2,645,000 to 2,935,000, effectively ending need for assistance (Blackard 1971).

Deer population sizes remain difficult to estimate and have great uncertainty, even with current modeling methods, so several states have discontinued population estimation (Adams and Ross 2015). Nonetheless, despite these limitations, estimates by state wildlife agencies represent the only consistent source of deer densities. Historical maps of deer densities in the southeastern United States from 1950, 1970, 1982, and 2005 are available, but maps remain inaccessible for comparisons if they are not digitized into GIS layers. Our objective was to document deer trends in the southeastern United States using available population sizes and deer density estimates from literature and digitized maps, which are accessible at the Forest Service data archive (<https://www.fs.usda.gov/rds/archive/>). We discuss implications of current deer densities for ecosystems, with acknowledgement of a continued research need to examine effects of deer on vegetation. This work is an extension of Hanberry and Hanberry (2020), for which we documented the methodology applied here to rapidly recover data from figures through conversion to GIS layers and compared deer densities from 1982 and 2005 maps of the continental United States.

METHODS

The Southeastern Cooperative Wildlife Disease Study, Department of Pathology and Parasitology, School of Veterinary Medicine, University of Georgia, Athens, Georgia, compiled southeastern United States maps of deer distribution and density using information obtained from state wildlife agencies, with map dates of 1950, 1970, and 1982 (<https://vet.uga.edu/scwds/range-maps>). The

Quality Deer Management Association assembled a continental United States map of white-tailed deer density and distribution from 2001 to 2005 (hereafter, 2003; Adams et al. 2009). These maps grouped deer densities into 4 colored classes: <5.8 deer/km², 5.8–11.6 deer/km², 11.6–17.4 deer/km², and >17.4 deer/km² (Fig. 1).

Following the methodology of Hanberry and Hanberry (2020), we imported map images of 1950 and 1970 deer densities into ArcGIS Pro (v2.2, ESRI, Redlands, CA, USA) and projected to Albers equal area conic, U.S. Geological Survey version. We georeferenced images to United States counties using a third order polynomial transformation. We imported georeferenced layers into eCognition (v9.3.2, Trimble, Westminster, CO, USA) and built image objects using multi-resolution segmentation with all bands weighted equally. We applied a small scale factor to minimize mixed color objects and delineate borders of deer density classes. We generated samples of each deer density class and additionally of no data values. We used a random forests classification based on mean and standard deviation of each color band (R Core Team 2018). We reclassified black objects (i.e., county names and line borders) using assign class algorithms in eCognition. We imported the classified object layer into ArcGIS Pro. We manually corrected any errors that persisted at the border of 2 color classes due to poor resolution and reclassified black color.

Following the methodology of Hanberry and Hanberry (2020), to estimate population numbers from the densities and distributions, we applied an approximate continental United States population estimate of 30 million at year 2000 to calibrate population estimates for the 2003 United States map (Webb 2014). To produce this value from the 2003 map, we used the least value for each density class (i.e., 5.8, 11.6, 17.4 deer/km²), except we used a value of 1.85 deer/km² for the low density class. We compared our estimates to those from Newsom (1969), Blackard (1971), Quality Deer Management Association (QDMA; Adams and Ross 2015), and Southeast Deer Study Group (2002–2006).

RESULTS

Overall in the southeastern United States, white-tailed deer population size increased from a minimum of <215,000 during 1915–1930 (Blackard 1971) to 304,000 by 1940 (Newsom 1969), 476,000 by 1950, 2.41 million by the 1960s (Newsom 1969), 2.94 million to 4.12 million by approximately 1970 (Blackard 1971), 6.17 million by 1982, to 10.79 million or about 12 million by approximately 2003 (for 2005 in Adams and Ross 2015 and Southeast Deer Study Group 2002–2006; Tables 1 and 2). Please note that similar results during 1982 and 2003 for the continental United States, including the southeastern states, are presented in Hanberry and Hanberry (2020). Mean deer densities in the southeastern United States increased from 0.22 deer/km² during 1940 (Newsom 1969), 0.35 deer/km² during 1950 (1950 map), 2.2 to 3.1 deer/km² during approximately 1970 (Blackard 1971, 1970 map), 4.6 deer/km²

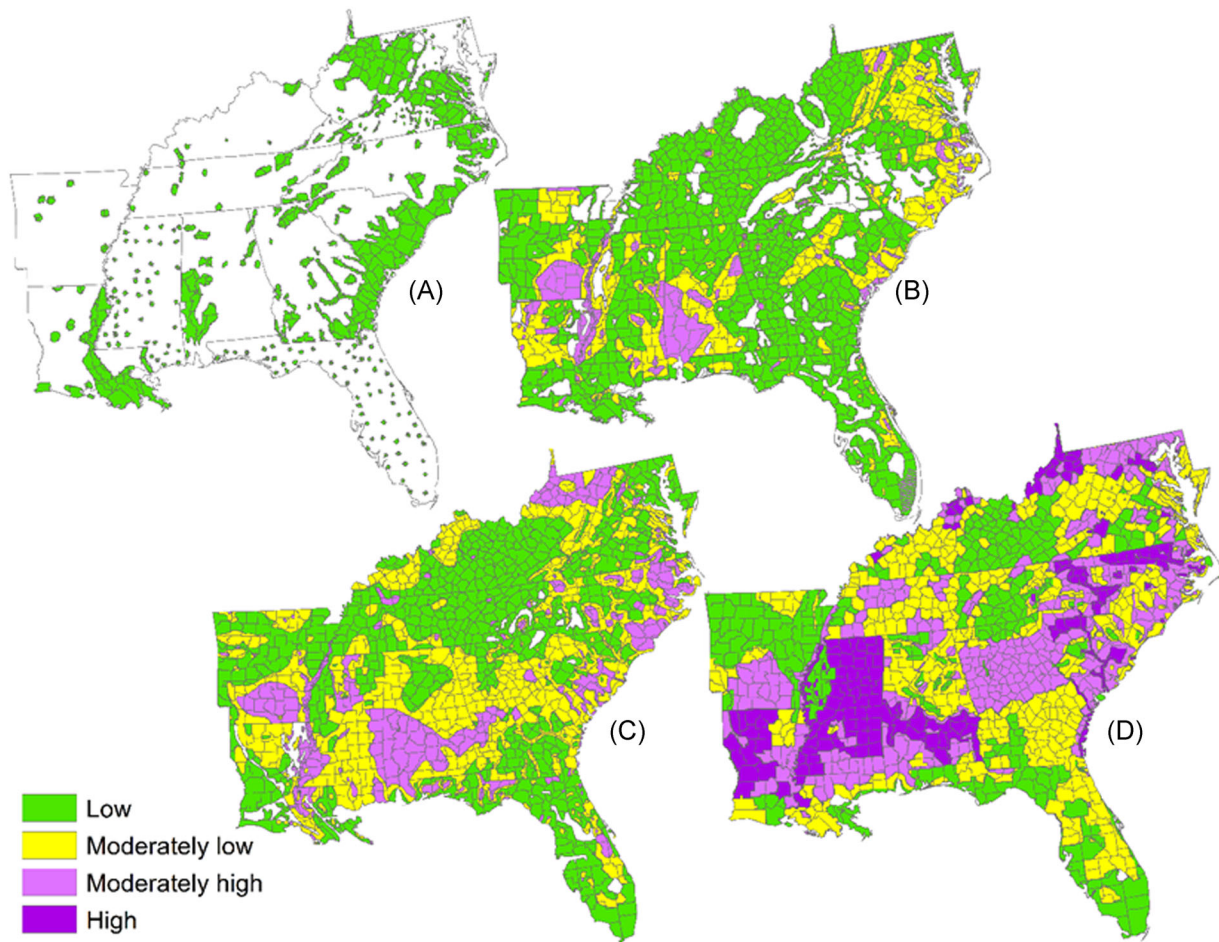


Figure 1. The 1950 (A), 1970 (B), 1982 (C), and 2003 (D; 2001 to 2005) deer densities in the southeastern United States, covering about 1.35 million km². The low-density class is <5.8 deer/km², the moderately low density class is 5.8–11.6 deer/km², the moderately high density class is 11.6–17.4 deer/km², and the high density class is >17.4 deer/km².

during 1982 (1982 map), to 8 deer/km² or 9 deer/km² during about 2003 (for 2005 in Adams and Ross 2015 and Southeast Deer Study Group 2002–2006). Statewide mean densities during 1950 ranged from 0.04 deer/km² and 0.05 deer/km² in Arkansas and Kentucky, respectively, to 0.9 deer/km² in South Carolina (Fig. 2). Deer increased to 3.5 deer/km² in Florida to 14.3 deer/km² in Mississippi during 2003.

Deer were present on 260,000 km² by 1950, 1.13 million km² by 1970, 1.29 million km² by 1982, and virtually the entire 1.35 million km² of the Southeast by 2003. Areas by state where deer were present increased from a range of about 3,000 km² in Kentucky and Arkansas to 47,000 km² in Virginia by 1950 to extents comparable with state size by 1970: 63,000 km² in South Carolina (the smallest state) to 140,000 km² in Georgia (the largest state).

Table 1. White-tailed deer population estimates in the southeastern United States from the 1950, 1970, and 1982 maps and published sources for the 1900s (Newsom 1969, Blackard 1971). Low values typically occurred during 1915–1930, and if unknown, then reported as less than the 1940 value.

State	Low value, Blackard	1940, Newsom	1950 map	1960s, Newsom	1969, Blackard	1970 map	1982 map
Alabama	1,000	15,000	44,240	350,000	450,000	683,530	960,480
Arkansas	<500	25,000	5,940	250,000	300,000	552,480	680,320
Florida	33,000	33,000	15,120	300,000	450,000	271,710	444,180
Georgia	<3,000	3,000	77,320	150,000	150,000	339,240	720,390
Kentucky	<2,000	2,000	5,350	65,000	65,000	180,110	320,540
Louisiana	15,000–20,000	67,000	71,950	200,000	300,000	410,320	424,450
Mississippi	<2,500	2,500	12,910	275,000	260,000	538,090	803,860
North Carolina	<50,000	50,000	65,970	370,000	370,000	356,610	737,340
South Carolina	<80,000	80,000	77,300	170,000	250,000	241,840	406,640
Tennessee	<1,000	1,000	13,910	75,000	90,000	179,050	285,840
Virginia	<25,000	25,000	86,200	200,000	250,000	368,650	390,180
Total	<215,000	303,500	476,210	2,405,000	2,935,000	4,121,630	6,174,220

Table 2. Comparison of white-tailed deer population estimates in the southeastern United States from the 2003 map with published sources (QDMA 2005, Southeast Deer Study Group [SDSG] 2002–2006).

State	2005 QDMA ¹	2003 SDSG	2003 map	QDMA to SDSG		QDMA to 2003 map		SDSG to 2003 map	
				Difference	Ratio	Difference	Ratio	Difference	Ratio
Alabama	1,750,000	1,750,000	1,313,020	0	1.00	436,980	1.33	436,980	1.33
Arkansas	875,000*	875,000	686,810	*	*	*	*	188,190	1.27
Florida	800,000*	800,000	525,210	*	*	*	*	274,790	1.52
Georgia	1,470,000	1,175,000	1,191,410	295,000	1.25	278,590	1.23	-16,410	0.99
Kentucky	847,911	875,000	518,650	-27,089	0.97	329,261	1.63	356,350	1.69
Louisiana	750,000	1,000,000	1,273,790	-250,000	0.75	-523,790	0.59	-273,790	0.79
Mississippi	1,700,000	1,562,500	1,767,950	137,500	1.09	-67,950	0.96	-205,450	0.88
North Carolina	1,111,000	1,072,750	1,285,590	38,250	1.04	-174,590	0.86	-212,840	0.83
South Carolina	800,000	925,000	807,740	-125,000	0.86	-7,740	0.99	117,260	1.15
Tennessee	965,125*	965,125	736,820	*	*	*	*	228,305	1.31
Virginia	1,000,000	955,000	682,330	45,000	1.05	317,670	1.47	272,670	1.40
Total	12,069,036	11,955,375	10,789,320	113,661	1.01	1,279,716	1.12	1,166,055	1.11

* Arkansas, Florida, and Tennessee estimates are from Southeast Deer Study Group 2002–2006.

Deer continued to expand to near complete distribution throughout all states by 1982 (Fig. 1).

Population estimates extrapolated from deer density maps generally aligned with estimates from other sources, although estimates may not be verified (Tables 1 and 2). During 2003, from the 2000–2005 map, the population estimate for the southeastern United States was 10.8 million deer compared to about 12 million deer from QDMA during 2005 (Adams and Ross 2015) and the Southeast Deer Study Group (2002–2006). In contrast,

values were high (by a factor of 1.4) during 1970, at 4.1 million deer, compared to 2.9 million deer total for 1969 by Blackard (1971).

DISCUSSION

We provided deer population sizes for states in the southeastern United States during approximately 1915–1930, 1940, 1950, 1960s, 1970, 1982, and 2001–2005 (Tables 1 and 2), density estimates, and digital maps of distributions during 1950, 1970, 1982, and 2001–2005. Total population

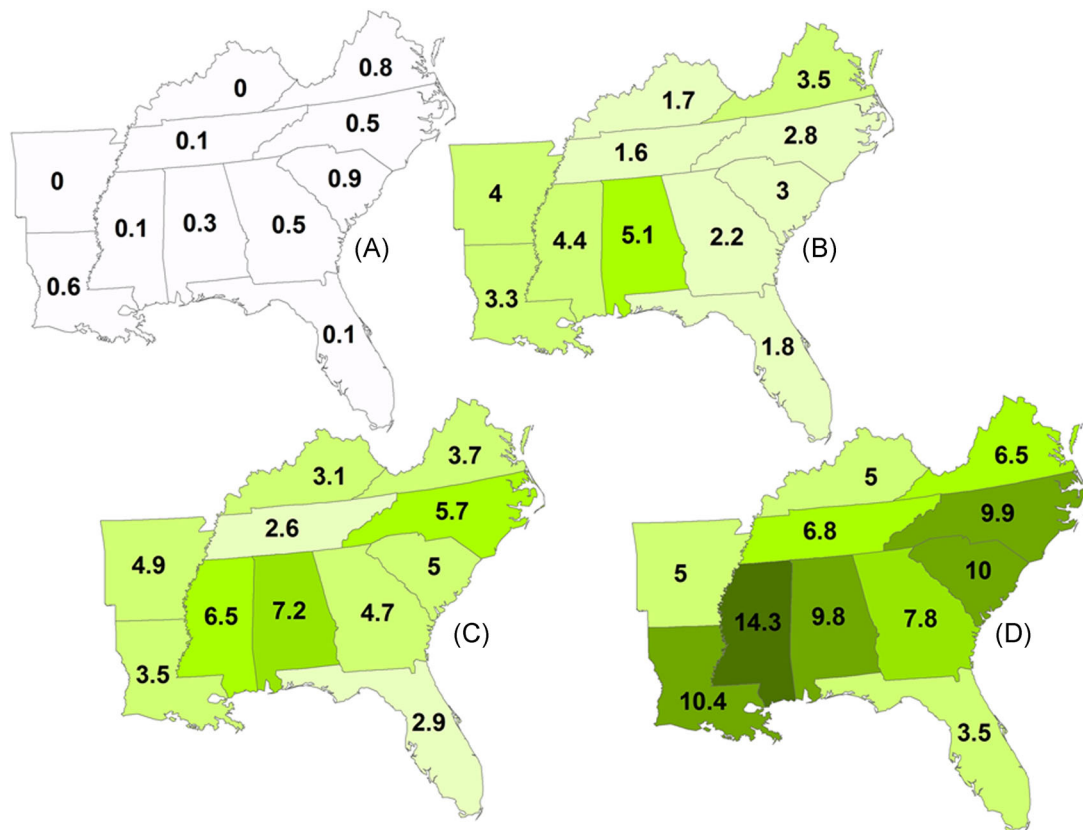


Figure 2. The 1950 (A), 1970 (B), 1982 (C), and 2003 (D; 2001 to 2005) mean statewide deer densities (deer/km²) in the southeastern United States (modified from Hanberry and Hanberry 2020).

size increased from a minimum of <215,000 during the early 1900s to 11 or 12 million deer by about 2003 to 2005, which corresponds to about 8 to 9 deer/km². The deer population generally has remained stable between 2005 and 2015 (Adams and Ross 2015). Current population estimates contain error and historical deer densities are even more uncertain.

Population estimates from distribution maps overall were similar to estimates from other sources, and may be no worse, considering the uncertainty involved. Nationwide estimates also matched well with other sources of estimates (Hanberry and Hanberry 2020). For the Southeast Deer Study Group (2002–2006), reported mean deer densities typically ranged considerably from year to year or did not change at all. During 2001–2005, we estimated a population of 10.8 million deer for the Southeast, comparable to 12 million deer reported by QDMA (Adams and Ross 2015) and Southeast Deer Study Group (2002–2006). Greater discrepancy occurred between estimates from the 1970 map and Blackard's (1971) estimates for 1969, at 4.1 million deer compared to 2.9 million deer. These errors may be due to applying a constant value of 1.85 deer/km² based on a combined low-density class, which represents values up to 5.8 deer/km². We did not find other sources of population estimates for comparison to 1950 and 1982 population estimates for the southeastern United States, although the nationwide estimate of 17 million deer for the 1982 map is comparable to 15 million deer by 1978 and 26 million deer by 1993 (Miller et al. 2003, Hanberry and Hanberry 2020). However, these estimates showed steady increases by decade and helped fill in data gaps.

One potential error may be decreased populations in Arkansas and Florida between 1940 and 1950. Nonetheless, limited locations of deer in these states during 1950 indicate that the population estimates may be relatively correct. According to the map, Arkansas had an equivalent area of deer presence as Kentucky (3,200 km² compared to 2,900 km², respectively), resulting in similar population estimates (5,900 and 5,400). Likewise, Florida and Tennessee had comparable area with deer (8,200 km² compared to 7,500 km², respectively). It may be that the 1950 map or 1940 estimates were incorrect, or that isolated populations fluctuated. Newsom (1969) and Blackard (1971) noted that small populations were vulnerable to pressures such as increased harvest during World War II and weather and disease events.

Historical deer densities were estimated conservatively by a contemporaneous expert at 4 to 8 deer per km² in the 5.2 million km² of eastern North America where white-tailed deer were most abundant, with localized areas that contained 20 to 40 or more deer/km² (McCabe and McCabe 1984). Given that the southeastern United States now averages 8 or 9 deer/km², current deer density is twice as great as conservative historical estimates, when based on minimum historical deer densities of 3.1 to 4.2 deer per km² (roughly 4 to 6 million deer; McCabe and McCabe 1984). Current mean deer densities here and

nationwide alternatively may be within pre-Euro-American settlement limits (Hanberry and Hanberry 2020). Although mid to high estimates may have been difficult to imagine from a perspective of near extirpation and deer restocking programs, moderately low deer densities of about 8 deer per km² historically would position current densities within moderate historical limits (McCabe and McCabe 1984). Moderately high deer densities of 12 and 16 deer/km² would represent populations of 16 and 21.5 million, respectively, perhaps setting an historical upper bound. However, land has changed since presettlement times and effectively the land base is smaller than the past, due to urbanization, residential use, and intensive agriculture.

Although there are limitations to both estimates and ecological inferences, if historical densities were at least 8 deer/km², similar to current deer densities, we suggest that it may be important to reevaluate thresholds at which white-tailed deer cause damage. Deer are considered a stressor that may drive vegetation dynamics, in particular reducing plant richness and abundance at threshold deer densities of 3 to 9 deer/km² (Alverson et al. 1988; Russell et al. 2001; McShea 2012; Ramirez et al. 2018). Research indicates that deer reduce regeneration of tree seedlings (Habeck and Schultz 2015, Ramirez et al. 2018). Nonetheless, other lines of evidence indicate minimal effect of deer on vegetation. Most tree seedlings will not survive with or without herbivores due to density-dependent mortality and variables affecting tree regeneration, including forestry practices, species, and soil fertility (Hanberry and Abrams 2019). Indeed, deer densities do not appear to be correlated with forest structure at landscape scales in the eastern United States (Hanberry and Abrams 2019). Forests of the southeastern United States have transitioned from woodlands to closed forests, perhaps doubling in tree densities (diameters ≥ 12.7 cm; Hanberry et al. 2018d). As for plant richness and abundance, after 5 years of deer exclusion during 2000 to 2005, no differences occurred beyond expected by random chance in 2 ecoregions of Mississippi with estimated densities of >20 deer/km² (Hanberry et al. 2014).

Furthermore, herbivory has influenced plants for millions of years and herbaceous plants thrived in historical forests of the eastern United States. The forb- and graminoid-dominated ground layer in frequently burned longleaf pine (*Pinus palustris*) forests of the southeastern United States was a diversity hotspot, with 25 to 35 species per m², whereas open oak (*Quercus* spp.) forests contained about 15 species per m² (Leach and Givnish 1999, Hanberry et al. 2018b). One misperception about historical forests of the southeastern United States may be that forbs, a component of deer forage, were not available within old-growth forests when indeed herbaceous plants formed the understory. For example, McCabe and McCabe (1984:19) specified that “deer thrived in forest edges, upland glades and riverine woodlands” but expressed uncertainty about deer

abundance “in the vast tracts of gentle topography that supported mature, virgin forest.” Similarly, Newsom (1969:1) wrote: “Obviously, most of the forested areas of the South were virgin wilderness, characterized by mature forests with relatively clean floors and little understory of value to deer.” Although historical forests of the southeastern United States were old-growth forests, they were predominantly comprised (~75%) of pine (*Pinus* spp.) and oak trees (Hanberry and Nowacki 2016; Hanberry et al. 2018c, d). Longleaf pine, shortleaf pine (*P. echinata*), and several upland oak species are fire-tolerant; thus, their historical dominance signifies a widespread historical fire regime (Hanberry et al. 2018a, b). Fire removed woody vegetation, allowing herbaceous vegetation to claim the understory and resulting in forested grasslands of savannas, open woodlands, and closed woodlands (Hanberry et al. 2018a, b). Plentiful forbs, with some amount of tree regeneration and shrub and vine presence, provided deer forage within forests.

Beyond herbivory, herbaceous plants have been under a variety of additional pressures since Euro-American settlement and fire exclusion during the first half of the 1900s. Namely, widespread increase in tree densities may exacerbate damaging effects of browsing because trees and other woody vegetation have claimed the understory, reducing herbaceous plants. Deer herbivory is a disturbance of herbaceous plants, but deer may be one of the few restraints on tree regeneration that is out-competing herbaceous plants for growing space and light.

Instead of a tree regeneration problem, we propose that deer may be considered a natural disturbance that help reduce tree densities, even though deer at current densities do not appear to be able to control great tree densities at landscape scales. Like other disturbances, deer regimes vary in intensity, with estimates of up to 40 deer/km² or more historically (McCabe and McCabe 1984). For example, even when deer were scarce during the 1940s, Leopold et al. (1947) documented problem areas of great deer densities. However, we recognize the need for continued research about the effects of deer on plant composition.

MANAGEMENT IMPLICATIONS

We compiled a history of deer population sizes in the southeastern United States between the early 1900s and early 2000s, supplemented by digitized maps. Regaining this information may be useful to deer managers and researchers. Estimates provide the best available information but may not be accurate due to lack of verification, particularly at localized spatiotemporal scales. Current densities are about 8 to 9 deer/km², and if historical densities were at least 8 deer/km², implications from this study include the research need to reevaluate thresholds at which deer cause damage. Herbivores are natural disturbances that have been removing plant biomass for millions of years, and despite herbivory, herbaceous plants have been successful in the southeastern United States.

ACKNOWLEDGMENTS

We thank K. Adams, QDMA, for providing deer density maps, and editors and reviewers for their time and comments. The authors received no funding; PH digitized the maps and BBH completed all other tasks. The authors have no conflicts of interest.

LITERATURE CITED

- Adams, K., R. J. Hamilton, and M. Ross. 2009. QDMA's whitetail report 2009. QDMA, Bogart, Georgia, USA.
- Adams, K., and M. Ross. 2015. QDMA's whitetail report 2015. QDMA, Bogart, Georgia, USA.
- Adams, K. P., and R. J. Hamilton. 2011. Management history. Pages 355–377 in D. G. Hewitt, editor. *Biology and management of white-tailed deer*. CRC Press, Boca Raton, Florida, USA.
- Alverson, W., D. Waller, and S. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* 2:348–358.
- Blackard, J. J. 1971. Restoration of the white-tailed deer in the southeastern United States. Thesis, Utah State University, Logan, USA.
- Habeck, C. W., and A. K. Schultz. 2015. Community-level impacts of white-tailed deer on understory plants in North American forests: a meta-analysis. *AoB Plants* 7:plv119.
- Hanberry, B. B., and M. Abrams. 2019. Does white-tailed deer density affect tree stocking in forests of the eastern United States? *Ecological Processes* 8:30.
- Hanberry, B. B., M. D. Abrams, and J. D. White. 2018a. Is increased precipitation during the 20th century statistically or ecologically significant in the eastern US? *Journal of Land Use Science* 13:259–265.
- Hanberry, B. B., D. C. Bragg, and T. F. Hutchinson. 2018b. A reconceptualization of open oak and pine ecosystems of eastern North America using a forest structure spectrum. *Ecosphere* 9:e02431.
- Hanberry, B. B., R. F. Brzuszek, H. T. Foster II, and T. J. Schauwecker. 2018c. Recalling open old growth forests in the Southeastern Mixed Forest province of the United States. *Écoscience* 26:11–22.
- Hanberry, B. B., K. Coursey, and J. S. Kush. 2018d. Structure and composition of historical longleaf pine ecosystems in Mississippi, USA. *Human Ecology* 46:241–248.
- Hanberry, B. B., and P. Hanberry. 2020. Rapid digitization to reclaim thematic maps of white-tailed deer density from 1982 and 2003 in the conterminous US. *PeerJ* e8262.
- Hanberry, B. B., and G. J. Nowacki. 2016. Oaks were the historical foundation genus of the east-central United States. *Quaternary Science Reviews* 145:94–103.
- Hanberry, P., B. B. Hanberry, S. Demarais, and B. D. Leopold. 2014. Impact by white-tailed deer on community biodiversity in Mississippi, USA. *Plant Ecology and Diversity* 7:541–548.
- Leach, M. K., and T. J. Givnish. 1999. Gradients in the composition, structure, and diversity of remnant oak savannas in southern Wisconsin. *Ecological Monographs* 69:353–374.
- Leopold, A., L. K. Sows, and D. L. Spencer. 1947. A survey of overpopulated deer ranges in the United States. *Journal of Wildlife Management* 11:162–177.
- McCabe, R. E., and T. R. McCabe. 1984. Of slings and arrows: an historical retrospection. Pages 19–72 in L. K. Halls, editor. *White-tailed deer: ecology and management*. Stackpole Books, Harrisburg, Pennsylvania, USA.
- McShea, W. J. 2012. Ecology and management of white-tailed deer in a changing world. *Annals of the New York Academy of Sciences* 1249:45–56.
- Miller, K. V., L. Muller, and S. Demarais. 2003. Pages 906–930 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, editors. *White-tailed deer. Wild mammals of North America: Biology, Management and Conservation*. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Newsom, J. D. 1969. Pages 1–4 in L. K. Halls, editor. *History of deer and their habitat in the south. White-tailed deer in the southern forest habitat*. USDA Forest Service Southern Forest Experiment Station, Nacogdoches, Texas, USA.
- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

- Ramirez, J. I., P. A. Jansen, and L. Poorter. 2018. Effects of wild ungulates on the regeneration, structure and functioning of temperate forests: a semi-quantitative review. *Forest Ecology and Management* 424: 406–419.
- Russell, F. L., D. B. Zippin, and N. L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1–26.
- Southeast Deer Study Group. 2002–2006. Proceedings. <<https://www.sedsg.com/proceedings.php>>. Accessed 19 Jun 2020.
- Webb, G. K. 2014. Results of environmental scanning applied to the design of a deer management decision support system (DSS) for the United States and California. *Issues in Information Systems* 2014:77–88.

Associate Editor: Ruckstuhl.