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To cite this article: Elic M. Weitzel (2021) Investigating overhunting of white-tailed deer (*Odocoileus virginianus*) in the late Holocene Middle Tennessee River Valley, Southeastern Archaeology, 40:1, 1-19, DOI: [10.1080/0734578X.2021.1873641](https://doi.org/10.1080/0734578X.2021.1873641)

To link to this article: <https://doi.org/10.1080/0734578X.2021.1873641>



Published online: 25 Jan 2021.



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Investigating overhunting of white-tailed deer (*Odocoileus virginianus*) in the late Holocene Middle Tennessee River Valley

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ABSTRACT

Resource depression – a decline in encounter rates with prey due to the actions of a predator – has been documented for numerous species in North America. Yet it is not fully understood whether white-tailed deer (*Odocoileus virginianus*), the most common prey species for Native peoples in eastern North America, were depressed prior to European colonization. To investigate whether white-tailed deer were depressed in precolonial eastern North America, I analyze zooarchaeological data from six sites in the Middle Tennessee River Valley. My results are equivocal, as different lines of evidence support conflicting interpretations. Declines in the abundance of deer in upland sites after ca. 4000 cal BP support depression of deer. However, deer did not decline in floodplain sites, perhaps due to anthropogenic environmental modification (i.e., burning). The upland decline coincides with a shift toward greater wetland patch use, which may have driven a reduction in deer hunting due to patch choice dynamics, not depression. Furthermore, declining deer abundance co-occurs with high terrestrial foraging efficiency, contrary to the expectation that greater exploitation of lower-ranked prey types should occur coincident with high-ranked deer declines. I find no clear support for resource depression of white-tailed deer in this region, but further analysis is needed.

ARTICLE HISTORY

Received 28 July 2020
Accepted 6 January 2021

KEYWORDS

Optimal foraging theory;
resource depression;
landscape management;
zooarchaeology; Dust Cave;
Russell Cave

Over the last 25 years, archaeologists have reported a wealth of evidence suggesting that various animal taxa were overhunted in the past. From artiodactyls in western North America (Broughton 2002; Broughton et al. 2010) to tortoises in the Near East (Stiner et al. 1999, 2000) and moa in New Zealand (Nagaoka 2002, 2005), this phenomenon of resource depression has been well documented around the world (Jones and Hurley 2017). Yet despite white-tailed deer (*Odocoileus virginianus*) being the most common faunal food resource in most eastern North American archaeological sites (Wolverton et al. 2008:2–3), the question of whether the species was depressed prior to European colonization has yet to be conclusively determined for much of eastern North America. In fact, some have argued that the species was never depressed at all (Smith 2009). To investigate whether white-tailed deer were depressed in precolonial eastern North America or whether they were resilient to depression, I analyze previously published zooarchaeological data from six sites in the Middle Tennessee River Valley (MTRV) spanning the last 13,000 years.

Resource depression refers to a reduced encounter rate with a prey type due to the actions of a predator, such as humans. Such depression can take any of three forms: *behavioral* in cases where prey alter their behaviors to avoid predation, *microhabitat* when prey relocate to avoid predation, or *exploitation* when their actual population is reduced through mortality (Charnov et al. 1976). Therefore, overhunting in the sense of prey population decline is only one form of resource depression (i.e., exploitation), and depression can occur for other reasons unrelated to prey mortality. I follow Wolverton et al. (2012:463) in subsuming microhabitat under behavioral depression, as these actions are not mutually exclusive and relocation is a behavioral strategy. This reduces the types of resource depression to two: behavioral and exploitation. Resource depression has long been a staple of zooarchaeological research (Broughton 1994a, 1994b), so much so that the sheer abundance of research concerned with resource depression has led many to mistakenly assume that optimal foraging theory studies are effectively synonymous with resource depression – an assumption that has been shown to be erroneous (Jones and Hurley 2017).

Despite abundant evidence for resource depression around the world, not all animal prey targeted by human hunters were exploited to the point of depression and some may have been quite resilient to it. Some populations of fish (Butler and Campbell 2004; Campbell and Butler 2010; Jones et al. 2016) and shellfish (Ulm et al. 2019), for example, have proved resilient to human predation through either intrinsic demographic attributes or other mitigating forces. Such phenomena are particularly well studied along the West Coast of North America, where many riverine and marine fisheries remained highly productive despite millennia of human predation (Campbell and Butler 2010; Jones et al. 2016). Some argue that this continued profitability was the result of deliberate Indigenous resource management with an eye toward long-term sustainability (Anderson 2005; Lightfoot et al. 2013; Lightfoot and Parrish 2009). It is also possible, however, that perceived sustainability was an epiphenomenal outcome of high resource replenishment rates and relatively low human population size, although there are certainly cases where sustainability resulted from ritually mediated rules of multigroup coordination (Jones and Codding 2019). Inadvertent, epiphenomenal conservation is also observed in ethnographic studies of contemporary foragers for whom long-term sustainable resource harvesting is not a stated goal, but a positive consequence of foraging practices that are aligned with traditional knowledge and understandings of the environment (Hunn 1993, 2014) and driven by human and resource population ecology (Bird et al. 2013; Bird et al. 2016b; Bliege Bird 2015; Bliege Bird et al. 2018; Codding et al. 2014). This distinction between deliberate and epiphenomenal conservation therefore appears to result from Western understandings of sustainability. Many Indigenous societies need not ascribe intentionality to the pursuit of conservation because it simply accompanies their worldview and foraging practices, making it appear unintentional to Western observers (Turner and Berkes 2006).

White-tailed deer

The white-tailed deer is one species argued to have been sustainably hunted by Indigenous peoples through time, and it is unclear just how widespread depression of this species may have been, if it occurred at all. In the late Pleistocene (>11,750 cal BP) and early Holocene (11,750–8000 cal BP), deer are known to have been relatively less abundant on North American landscapes. Broughton et al. (2008) argue that greater seasonality during this period in western North America reduced artiodactyl populations, including those of the mule,

or black-tailed, deer (*Odocoileus hemionus*), a close relative of the white-tailed deer. Artiodactyl populations did not increase until well into the middle Holocene (8000–4000 cal BP). Wolverton et al. (2008:2; Wolverton et al. 2009b) argue, however, that white-tailed and mule deer were less abundant at the end of the Pleistocene due to competition with megaherbivores and became more common in the Holocene as these species went extinct. Whatever the cause, white-tailed and mule deer are indeed uncommon in archaeological assemblages until the middle Holocene (Broughton and Bayham 2003; Broughton et al. 2008; Byers and Broughton 2004; Weitzel 2019; Wolverton et al. 2008:2).

It has been suggested that the white-tailed deer is somewhat of an anomaly compared to other North American artiodactyls. In western North America, depression of their close relative, the mule deer, has been documented (Broughton 2002; Broughton et al. 2010; Cannon 2000, 2003; Codding et al. 2010). In California (Fisher 2018) and New Mexico (Jones 2016), mule deer were depressed by Native hunters but rebounded after European colonization. Mule deer have been known to form relatively large herds for protection against predators and vacate their home ranges in response to heavy predation – both forms of behavioral depression (Wolverton et al. 2012:471).

In contrast, it has been argued that behavioral depression of white-tailed deer is less likely (Wolverton et al. 2012), and perhaps much less so (Smith 2009). Relative to other North American ungulates such as the mule deer, white-tailed deer live in small groups or are solitary, meaning that forming herds as a means of predator defense occurs only rarely (DeYoung and Miller 2011:313, 319). They also exhibit strong philopatry (Etter et al. 2002; Grund et al. 2002; Lesage et al. 2000; Rhoads et al. 2010; Wolverton et al. 2012:468) in small (but somewhat variable) home ranges (Brinkman et al. 2005; Kilpatrick and Spohr 2000; Lesage et al. 2000; Rouleau et al. 2002; Walter et al. 2011) and because dispersal is often risky (Berlinger et al. 2002; Nixon et al. 2001), they are often reluctant to leave their home range or shift habitat use even under predation (Karns et al. 2012; Roseberry and Woolf 1998; Wolverton et al. 2012:468–471). Even after several individuals in New York were experimentally culled, tracking data showed that no adjacent deer took advantage of the newly available territories by adjusting their home ranges (McNulty et al. 1997). Newly available territories typically remain vacant until filled by dispersing yearlings (Nixon et al. 1991).

As their high fidelity to their home-range precludes long-distance escape from predators, the antipredator behaviors of the white-tailed deer involve alerting

conspecifics (and predators) through vocalizations or stamping, hiding in thick cover, fleeing short-distances through vegetation cover to break the predator's line of sight, and luring predators away from fawns (DeYoung and Miller 2011:319; Geist 1998:283; Wolverton et al. 2012:467–468). White-tailed deer can become behaviorally depressed by avoiding roads and open areas and increasing their nocturnal activity in response to human hunting (DeYoung and Miller 2011:320–321). Still, all of these strategies occur within small home ranges that would also be familiar to hunters, and white-tailed deer rarely leave their home ranges for long periods of time in response to human predation (DeYoung and Miller 2011:320–321). For these reasons, Wolverton et al. (2012) suggest that behavioral depression of white-tailed deer is unlikely to have occurred in much of precolonial North America. As such, exploitation depression is argued to have been the most likely mechanism behind declining encounters with deer in the past.

Yet even exploitation depression of deer has been questioned, with some arguing that white-tailed deer would have been “invulnerable to overexploitation” (Smith 2009:170). Deer can, in certain cases, persist under remarkably high rates of predation, with maximum sustainable annual harvest ranging up to 26.6% and a maximum allowable yield of 37.3% in simulation models (Whitaker 2009). Sustainable harvest rates of 33% are reported for a deer population in Michigan, while rates of 44% led to population decline (Van Etten et al. 1965). Sustainable rates of 55% for males and 21% for females are reported in a growing population in Illinois (Nixon et al. 1991). Nevertheless, rates of 43% and 22% respectively in Minnesota (Fuller 1990) and experimental harvests of 9%–27% in Texas led to declines in these deer populations (DeYoung 2011:172). Clearly, the sustainable harvest of deer depends on a host of ecological factors, but in certain cases their populations can withstand high mortality.

Furthermore, white-tailed deer have high reproductive potential (DeYoung 2011:149), with high fertility rates (Wolverton et al. 2012:464–465) alongside high fawn mortality (Campbell et al. 2005). Populations can grow rapidly even in the face of high mortality as long as fawn recruitment rates are high enough. Fawn recruitment can even increase when populations are stressed, possibly counteracting some of the effects of exploitation (Beringer et al. 2002). Reduced competition with conspecifics can result in increased fawn body weights and improved health and nutrition (Ballard 2011:254). Older and larger females tend to be in better somatic and nutritional condition, thus birthing more fawns and better ensuring fawn survival by possessing

nutrients necessary to sustain lactation (Ditchkoff 2011:46–47). Deer body size may decline due to greater competition for resources when population density increases (Ballard 2011:254; Wolverton et al. 2007). Thus, populations of larger deer under low to moderate predation could theoretically have higher fawn recruitment rates. Based on these observations, some have hypothesized that white-tailed deer may never have experienced any sort of depression – behavioral or exploitation – in precolonial North America and that they provided a sustainable food source for Native populations through time (Smith 2009; Wolverton et al. 2008:19).

In addition to their physiology and behavior, the precolonial abundance of white-tailed deer may have been impacted by ecological facilitation by humans in the form of environmental modification. Facilitation (Bronstein 2009; Bruno et al. 2003) refers to ecological interactions like mutualism and commensalism, in which at least one party benefits and the other either benefits or is unaffected. White-tailed deer thrive in disturbed, early successional and ecotonal forest edge habitats with a high degree of heterogeneity and access to woody understory vegetation that provides both forage and cover (Foster et al. 1997; Nixon et al. 1991; Rhoads et al. 2010; Seagle 2003; Stewart et al. 2008, 2011:186, 188–190). Anthropogenic disturbance produces exactly this type of habitat (Bird et al. 2005, 2016a, 2016b; Bliege Bird et al. 2008; Bliege Bird 2015; Stewart et al. 2011:189–190). Native peoples in eastern North America are known to have managed their environments through forest clearing and burning, particularly by the late Holocene (4000–0 cal BP) as human populations rapidly grew and horticultural economies spread (Delcourt and Delcourt 1997, 1998; Delcourt et al. 1986, 1998; Denevan 1992, 2011; Hammett 1992:29–30). Such environmental modification may have promoted deer populations. Yerkes (2005:248–249) argues that such anthropogenic landscape changes in the midwestern United States may have counteracted predation on deer and prevented resource depression, and this sentiment has been echoed by others (Smith 2009).

Despite these theoretical arguments for the resilience of white-tailed deer to resource depression, modern ecological studies show that they can certainly be depressed, both by humans and nonhuman predators (Ballard 2011; DeYoung 2011). However, depression of deer when human populations were smaller in the archaeological past is a different matter, and evidence is more limited. In southeastern Texas, Wolverton et al. (2008) found evidence for intensified deer exploitation throughout the Holocene as evidenced by changes in deer age profiles and processing intensity.

This evidence is consistent with greater harvest pressure. To infer changes in deer abundance, Wolverton et al. (2007) analyzed deer body size under the theoretical assumption that larger population size will increase resource competition and selective pressures between individuals, resulting in smaller-sized adults. They found that deer in precolonial Texas were larger than contemporary deer that are not hunted and are the same size as contemporary deer populations that are hunted. That precolonial deer were relatively large suggests that deer were less numerous prior to European colonization due to Native hunting pressure, and today, overabundance of deer (McShea 1997) has led to general size diminution (Wolverton et al. 2007), though exceptions to this pattern exist and can be explained by geographic variation in food availability (Wolverton et al. 2009a). Subsequent analyses of deer abundance relative to the abundance of smaller game species in the region corroborated this pattern. Declining abundance of white-tailed deer through time was also associated with increased transport of low-utility skeletal portions to human habitation sites and greater fragmentation of bones for grease and marrow extraction. This intensification of deer hunting is argued to have resulted from exploitation depression, as behavioral depression would not impact the age structure of the prey population (Wolverton et al. 2012).

While Wolverton et al.'s (2007, 2008, 2012) work demonstrates that depression of white-tailed deer is possible, clear evidence of such depression is lacking outside of Texas. Styles and Klippel (1996) investigate the abundance of deer in Midwestern archaeological sites and show that their abundance peaks ca. 5–6,000 cal BP in the lower Illinois River valley and ca. 2–3,000 cal BP in the central Mississippi River valley before declining through the Mississippian period (1000–500 cal BP). However, Yerkes (2005) notes that deer remains are relatively abundant at several Mississippian sites in the region, particularly from autumn and winter occupations, and infers that “there is little evidence that Mississippian hunting ‘pressure’ had an adverse effect on American Bottom deer populations” (Yerkes 2005:248). These conflicting lines of evidence make it difficult to evaluate whether white-tailed deer were indeed sustainably harvested at high rates through time, or whether they were depressed by human hunting prior to European colonization in much of eastern North America.

Predictions

Given the established increase in deer populations from the early to middle Holocene, the ecology of deer

physiology and behavior, and the growth of human populations and increasing landscape modification in the late Holocene, several outcomes are possible for white-tailed deer populations in precolonial eastern North America. It is possible that deer abundance may have increased from the early to middle Holocene and remained stable through the late Holocene if deer were sustainably harvested by Native hunters. While the late Holocene witnessed the highest human population levels in the region, if Smith (2009) is correct, they were still not high enough to depress white-tailed deer. It is alternatively possible that deer abundance may have increased into the middle Holocene, then declined during the late Holocene due to resource depression driven by a growing human population. It is possible, if not likely, that such a decline in deer abundance in the late Holocene would not have been universal but occurred only in some areas and not others depending on local human density and predation intensity.

However, it is perhaps most plausible that deer abundance was spatially heterogeneous. Given that Native populations mainly concentrated in river valleys and the coastal plain in eastern North America (Anderson 1990; Anderson et al. 2007; Anderson and Sassaman 2012), these areas may have experienced the greatest anthropogenic disturbance. Therefore, if deer abundance did decline in the late Holocene due to anthropogenic resource depression, it is possible that either (a) deer declined only in floodplain and coastal plain habitats due to greater hunting pressures from higher human population density in such locations, or (b) that deer were facilitated in floodplains and coastal plains by anthropogenic disturbance but were depressed in uplands where ecosystem disturbance was less common.

Materials and methods

To test these various hypotheses, I used previously published faunal data from six sites in the Middle Tennessee River Valley of northern Alabama and southern Tennessee spanning the last 13,000 years (Table 1; Weitzel 2019). The Middle Tennessee River Valley is an ideal place to investigate white-tailed deer depression in precolonial times (Figure 1). Relative to surrounding areas, the MTRV sustained comparatively high human populations throughout much of the precolonial period, from the Paleoindian period (Anderson et al. 2010) to the Shell Mound Archaic (Bissett 2014) and beyond (Miller 2018). Furthermore, palynological records from the valley, as well as the surrounding region, indicate the existence of anthropogenic landscape

Table 1. Number of Identified Specimens (NISP) for relevant taxa from each context.

Midpoint Date (cal BP)	Site	Wetland NISP	Terrestrial NISP	Deer NISP	Squirrel NISP	Sum NISP (Identified to Order and below)
400	Russell Cave	57	167	70	29	291
1050	Widow's Creek	615	431	223	110	1144
1100	Mussel Beach	2	1	1	0	6
1300	Russell Cave	105	198	108	18	347
1700	Mussel Beach	23	46	36	7	71
2000	LaGrange Shelter	14	7	3	0	28
2150	Russell Cave	77	88	48	6	173
2300	Widow's Creek	76	48	21	14	137
2650	Mussel Beach	15	15	13	0	37
3150	Stanfield-Worley Shelter	87	371	260	73	618
4200	Russell Cave	26	79	52	9	123
4300	Mussel Beach	1	1	1	0	2
4450	Widow's Creek	29	22	13	5	60
6100	Dust Cave	23	33	16	12	77
7700	LaGrange Shelter	1	3	3	0	7
7750	Dust Cave	108	176	62	67	391
7800	Russell Cave	37	217	93	49	302
8900	Dust Cave	77	94	8	73	220
9100	Russell Cave	89	1360	140	789	1581
9500	Dust Cave	23	27	6	10	69
9620	Stanfield-Worley Shelter	5	228	162	58	297
10900	LaGrange Shelter	1	5	2	0	13
11600	Dust Cave	113	92	24	44	248
12150	Dust Cave	178	91	19	20	407

management in the form of burning in the middle and late Holocene (Chapman et al. 1982; Delcourt et al. 1983, 1986, 1998; Delcourt and Delcourt 1997, 1998).

Site descriptions

The assemblages analyzed here originate from the sites of Dust Cave, Mussel Beach, Widow's Creek, Russell Cave, Stanfield-Worley shelter, and LaGrange shelter. The occupations of these six sites span the last 13,000 years, from the terminal Pleistocene to the late Holocene. In most cases, the contexts of zooarchaeological materials from these sites have associated radiocarbon dates, but some contexts were dated relatively using artifact typologies. I use the midpoint date of each component in my analyses – the calendar date halfway between the earliest and latest calibrated radiocarbon date, or when no absolute dates were available, the midpoint date of the culture history period assigned to the component by the original excavators. Given that only number of identified specimen (NISP) values are consistently provided in the reports and publications on these faunal assemblages, I restrict my analysis to using this metric instead of others such as the minimum number of individuals (MNI).

Dust Cave (1Lu496). Dust Cave is located on the floodplain of the Tennessee River in northwestern Alabama (Figure 1). The site has been radiocarbon dated to between 12,700 and 5600 cal BP, ranging from the Younger Dryas to the middle Holocene (Sherwood et al. 2004). Dust Cave was excavated between 1989 and 2002, and all materials were water screened through

6-mm (1/4-in) mesh (Sherwood et al. 2004) except those from flotation samples that were screened through 1.4-mm and 0.7-mm mesh (Carmody 2009, 2010; Hollenbach 2005, 2009). Faunal remains were identified by Walker (1998) and Weitzel (2019), with a total vertebrate archaeofaunal assemblage of 12,998 specimens (NSP) of which 46% (NISP = 6,043) were identifiable to at least Class and 11% (NISP = 1,412) were identifiable more specifically than Class (Table 1). These remains originate from six radiocarbon dated cultural components (Sherwood et al. 2004): Benton (6500–5600 cal BP; NISP = 260), Eva/Morrow Mountain (8400–6000 cal BP; NISP = 1,236), Kirk (10,200–7800 cal BP; NISP = 759), Mixed Kirk (9600–9400 cal BP; NISP = 210), Early Side-Notched (12,000–11,000 cal BP; NISP = 1,073), and Paleoindian (12,650–11,200 cal BP; NISP = 2,505).

Mussel Beach (40Mi70). Mussel Beach is located directly on the Tennessee River near the border of Tennessee, Alabama, and Georgia (Figure 1). The site was occupied through the late Holocene (5500–900 cal BP) and was periodically excavated in the 1980s, 1991, 2009, and 2010. Sediments were screened through 6-mm (1/4-in) mesh, while finer mesh (2 mm) was used for flotation samples (Gregory et al. 2011). A small assemblage of vertebrate faunal remains (NISP = 116) was identified from four radiocarbon dated contexts spanning 4300–900 cal BP (Table 1). These contexts are the Late Archaic II (4300 cal BP; NISP = 2), Late Archaic III (2600 cal BP; NISP = 37), Middle Woodland (1700 cal BP; NISP = 71), and Late Woodland (1100 cal BP; NISP = 6).

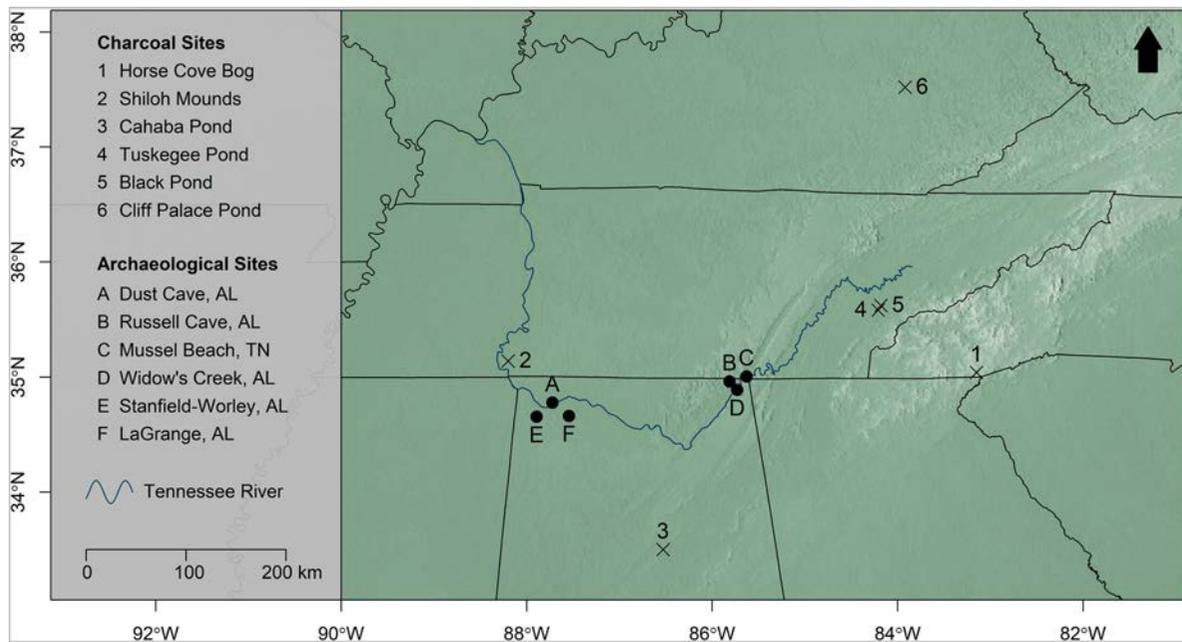


Figure 1. The locations of the six archaeological sites in the Middle Tennessee River Valley (MTRV) discussed in the text, along with six pollen core sites from the region yielding data on charcoal concentrations and influx through time.

Widow's Creek (1Ja305). The Widow's Creek site lies on the Tennessee River in northeastern Alabama (Figure 1). The occupation of the site spans 4500–1000 cal BP during the late Holocene (Morey 1996). Archaeologists from the University of Tennessee at Chattanooga excavated the site in the summer of 1973 using arbitrary 0.5-ft levels within 10-ft by 10-ft units. A 2-ft by 2-ft column from each unit was water screened through 6-mm (1/4-in) and 1.6-mm (1/16-in) mesh as were the sediments from all features (Olinger 1975; Warren 1975). Twenty-four features yielded vertebrate faunal remains (NISP = 1,341; Table 1). These features were relatively dated to three cultural components due to a lack of radiocarbon dates: Late Archaic (NISP = 60), Early Woodland (NISP = 137), and Middle/Late Woodland (NISP = 1,144; Morey 1996). The midpoint dates from each of these cultural periods were used here (Table 1).

Russell Cave (1Ja181). Russell Cave is located on a small tributary stream of the Tennessee River, about seven miles from the river itself (Figure 1). The occupation of the cave spans much of the Holocene (9600–400 cal BP; Griffin 1974). Weigel et al. (1974) report 30,000 vertebrate remains, from 66 different species, but only 10% (NISP = 2,891) of these were identifiable to a taxonomic category (Table 1). Sediments were dry screened through 6-mm (1/4-in) mesh, but those from greater depths were water screened through 6-mm (1/4-in) mesh, as soil moisture at these depths made dry screening ineffective (Griffin 1974:11–12). Faunal

remains originated from radiocarbon dated zones labeled G (9600–8200 cal BP; NISP = 1,581), F (8700–6900 cal BP; NISP = 302), E (6300–2000 cal BP; NISP = 123), D (2150 cal BP; NISP = 173), C (1400–1100 cal BP; NISP = 347), and B (400 cal BP; NISP = 291). Zone A (NISP = 74) was deemed to be modern in origin by the excavators and is therefore excluded from this analysis.

Stanfield-Worley (1Ct125). Stanfield-Worley Bluff Shelter is also located approximately seven miles from the Tennessee River in the uplands of northern Alabama (Figure 1). Materials from the site were screened through 6-mm (1/4-in) mesh by hand and mechanical agitation (DeJarnette et al. 1962; Hollenbach 2005:70–75) during excavation between 1960 and 1963. The original excavators separated the site's stratigraphy into two zones, D and A, based on artifact typologies. Hollenbach (2005:Table 4.2) revisited the site more than 40 years later and dated Zone D to between 11,700 and 7600 cal BP. The overlying zone, A, represents a late Holocene occupation of the site and was never radiocarbon dated. Therefore, the midpoint date for the late Holocene is used here. Parmalee (1962) identified 915 vertebrate faunal remains from 13 species: 297 from Zone D and 618 from Zone A.

LaGrange (1Ct90). LaGrange Bluff Shelter is located in northwest Alabama, several miles south of the Tennessee River on the side of a mountain (Figure 1). The site was excavated between 1972 and 1975, with all sediments screened through 6-mm (1/4-in) mesh

(DeJarnette and Knight 1976). Artifact typologies suggest that the site was used from the terminal Pleistocene through the late Holocene. Thirty years after the initial excavations, Hollenbach (2005:Table 4.5) returned to radiocarbon date Zone E (11,500–11,200 cal BP) and Zone C (8300–8400 cal BP). The site yielded a small faunal assemblage of only 48 identified specimens from three stratigraphic zones: Zones A (Woodland to Mississippian; NISP = 28), B (Early Archaic to Late Archaic; NISP = 7), and D (Late Paleoindian to Early Archaic; NISP = 13; Curren 1976). Because no radiocarbon dates were obtained for these three zones, the midpoint dates used herein were derived from the ascribed cultural history periods (Table 1).

Analyses of faunal abundance

To model changes in deer abundance through time, I calculated the proportion of deer bones (PD) in each assemblage by dividing the number of identified specimens (NISP) of white-tailed deer by the summed NISP of all vertebrate specimens identified to at least order (Table 2). Doing so prevents unidentified deer

bones (labeled as “Mammalia” or “Large Mammal,” for example) from being double-counted in the index. It is important to consider that a decline in the PD in these assemblages could result from factors other than depression, such as patch use choices by human foragers. If, for example, foragers shifted toward greater use of wetland as opposed to terrestrial patches, this could result in a decline in the PD as such a measure is not patch-specific. Greater exploitation of wetland vertebrates, even with no change in deer abundance (the PD), could reduce the PD in assemblages by increasing the denominator in such a calculation even if deer themselves were no less abundant on the landscape. If this were the case, a shift toward wetland patch use should be observed concurrent with any declines in the PD.

To ensure that no other foraging behaviors are driving any observed changes in the PD, I also examined patch use with a Patch Use Index (PUI). This index divides the sum NISP of all terrestrial fauna by the sum NISP of all wetland fauna (Table 2). When the PUI is high, relatively more terrestrial taxa are being taken than wetland (aquatic and semiaquatic) taxa, and vice versa. I divided the fauna in this study into two patches, termed wetland and terrestrial, based on the habitat classifications of common eastern North American fauna by O’Brien and Wood (1995). The wetland patch contains aquatic and semiaquatic taxa: all species of geese, swans, ducks, other waterfowl (e.g., loons), beavers (*Castor canadensis*), muskrats (*Ondatra zibethicus*), river otters (*Lontra canadensis*), minks (*Neovison vison*), amphibians, fishes, aquatic turtles, and also terrestrial animals that have strong preference for wetland habitats such as raccoons (*Procyon lotor*) and swamp rabbits (*Sylvilagus aquaticus*). The terrestrial patch contains white-tailed deer, tree squirrels (*Sciurus* sp.), groundhogs (*Marmota monax*), eastern cottontail rabbits (*Sylvilagus floridanus*), box turtles (*Terrapene carolina*), Phasianidae such as prairie chickens (*Tympanuchus* sp.) and turkeys (*Meleagris gallopavo*), and bobwhite quail (*Colinus virginianus*).

In addition to the PUI, measures of patch-specific foraging efficiency can also assist in identifying deer depression because such a process should result in reduced terrestrial patch foraging efficiency. Foraging efficiency refers to the benefits (typically kilocalories) gained by a forager per unit time while foraging for all prey types in their diet set (Broughton 1994a, 1994b; Coddling and Bird 2015). I therefore calculated a Deer-Squirrel Index (DSI) which divides the NISP of deer by the sum NISP of deer and squirrel (*Sciurus* sp.) as a proxy for terrestrial patch foraging efficiency (Table 2). Deer are the highest-ranked prey type in the

Table 2. Index values for each faunal context.

Midpoint Date (cal BP)	Site	Proportion Deer	Patch Use Index	Deer- Squirrel Index
400	Russell Cave	0.24	0.75	0.71
1050	Widow's Creek	0.19	0.41	0.67
1100	Mussell Beach	0.17	0.33	1.00
1300	Russell Cave	0.31	0.65	0.86
1700	Mussell Beach	0.51	0.67	0.84
2000	LaGrange	0.11	0.33	1.00
2150	Russell Cave	0.28	0.53	0.89
2300	Widow's Creek	0.15	0.39	0.60
2650	Mussell Beach	0.35	0.50	1.00
3150	Stanfield- Worley	0.42	0.81	0.78
4200	Russell Cave	0.42	0.75	0.85
4300	Mussell Beach	0.50	0.50	1.00
4450	Widow's Creek	0.22	0.43	0.72
6100	Dust Cave	0.21	0.59	0.57
7700	LaGrange	0.43	0.75	1.00
7750	Dust Cave	0.16	0.62	0.48
7800	Russell Cave	0.31	0.85	0.65
8900	Dust Cave	0.04	0.55	0.10
9100	Russell Cave	0.09	0.94	0.15
9500	Dust Cave	0.09	0.54	0.38
9620	Stanfield- Worley	0.55	0.98	0.74
10900	LaGrange	0.15	0.83	1.00
11600	Dust Cave	0.10	0.45	0.35
12150	Dust Cave	0.05	0.34	0.49

MTRV assemblages, meaning that they offer the greatest number of calories per unit time upon encounter. In contrast, squirrels are a low-ranked prey type offering a much lower caloric return rate (Weitzel 2019:197–200). A high DSI value therefore indicates that proportionately more high-ranked deer were taken by foragers relative to low-ranked squirrels. In combination with an overall decline in deer abundance, a decline in the DSI would be consistent with deer depression as optimal foraging theory asserts that increased exploitation of low-ranked prey types is a function of high-ranked prey abundance. Alternatively, if the DSI increases or remains constant, any observed decline in overall deer abundance (the PD) may more likely relate to patch choice dynamics rather than resource depression.

As it is possible that uplands and floodplains experienced different trends in deer population, patch use, and foraging efficiency, I created separate models for each setting. The sites of Dust Cave, Mussel Beach, and Widow's Creek are located on the floodplain of the Tennessee River and are thus modeled separately from the sites of Russell Cave, Stanfield-Worley shelter, and LaGrange shelter, which are located in the uplands.

I modeled temporal changes in deer abundance (PD), patch use (PUI), and terrestrial patch foraging efficiency (DSI) using binomial-family generalized linear models with second degree polynomials to permit the possibility of a directional change in the model fit. In doing so, I treat the data analyzed herein as ratio scale, as abundance index values are continuous and bounded by 0 and 1. These models were weighted by sample size so that, for example, an assemblage with 200 specimens would influence the model twice as much as an assemblage with 100 specimens. This permits me to avoid making arbitrary decisions about minimum required sample sizes and thereby include all assemblages in my analysis while statistically controlling for the biasing effects of sample size. The reader is therefore cautioned to avoid interpreting patterns in individual data points themselves and should focus instead on the model fit in each case. Model goodness of fit (i.e., effect size [Wolverton et al. 2016]) was measured using the deviance-squared (D^2) statistic: a maximum likelihood analogue of the better-known R^2 statistic (Guisan and Zimmermann 2000) calculated using the **modEvA** package (Barbosa et al. 2016). Statistical significance of models was determined via likelihood ratio tests (LRT) comparing fitted models to intercept-only forms using a chi-squared distribution. The data on deer abundance, patch use, and terrestrial foraging efficiency to which these models were fitted are provided in Table 1. Each site is comprised of multiple dated

components, for which the midpoint date is used here following the methodology of Weitzel (2019). All analyses were conducted in R (R Core Team 2019), and all data and code are available as supplementary information (Supplementary Files 1–6) and at DOI 10.17605/OSF.IO/9ZV6C.

Results

My results show that changes in deer abundance were not uniform across the landscape. The model of the proportion of deer (PD) over time for floodplain sites (Figure 2a) shows an increase through time with no evidence of declining abundance of white-tailed deer (LRT: $X^2 = 100.3$, $df = 2$, $p < 0.0001$; $D^2 = 0.61$). This is not consistent with depression but may suggest that deer were indeed resilient to depression, perhaps due to the positive effects of anthropogenic landscape modification or its own unique physiology or behavior. In the uplands, however, the model of PD (Figure 2a) increases from the terminal Pleistocene through the middle Holocene, but then decreases after ca. 4000 cal BP (LRT: $X^2 = 128.6$, $df = 2$, $p < 0.0001$; $D^2 = 0.25$), consistent with depression.

Models of patch use through time (the PUI) for both floodplain and upland sites (Figure 2b) suggest that a shift from terrestrial to wetland patch use occurred coincident with this decline in deer abundance (PD) in both floodplain (LRT: $X^2 = 54.5$, $df = 2$, $p < 0.0001$; $D^2 = 0.68$) and upland sites (LRT: $X^2 = 368.73$, $df = 2$, $p < 0.0001$; $D^2 = 0.82$). Patch choice dynamics may therefore be implicated in the apparent declines in deer in upland sites.

Additionally, no declines in terrestrial patch foraging efficiency, measured by the DSI, are observed (Figure 2c) for either floodplain (LRT: $X^2 = 79.7$, $df = 2$, $p < 0.0001$; $D^2 = 0.55$) or upland (LRT: $X^2 = 440.2$, $df = 2$, $p < 0.0001$; $D^2 = 0.52$) sites: terrestrial resource foraging efficiency increases monotonically through time in both models.

Discussion

Taken together, these results are equivocal and do not clearly suggest either depression or resilience of white-tailed deer to human activities. While PD does decline in upland sites in the MTRV, supporting resource depression of the species, the PUI suggests this apparent decline may be spurious and potentially driven by a shift toward greater wetland patch use in the late Holocene. Furthermore, the declining proportion of deer in upland sites is unaccompanied by a concomitant decline in terrestrial foraging efficiency (the DSI), which would be

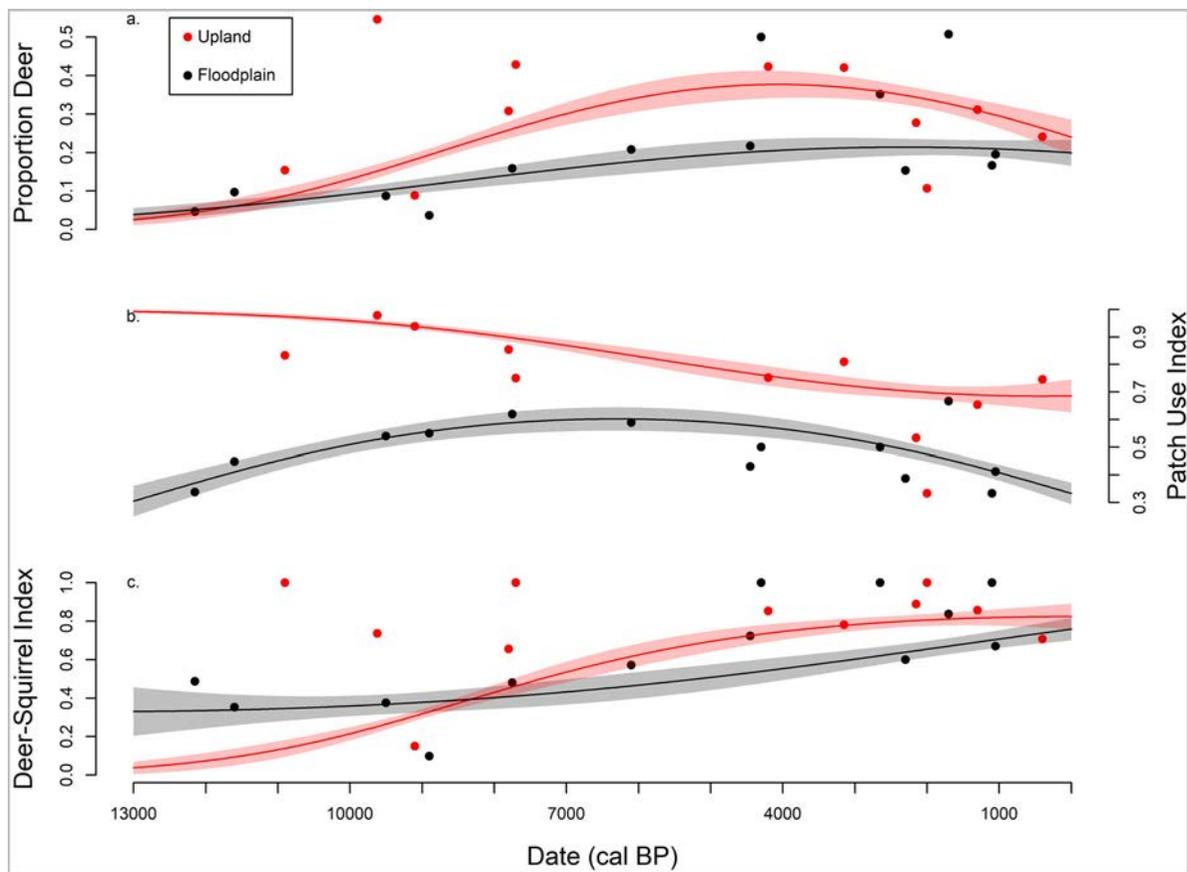


Figure 2. Models of (a) the proportion of deer (PD), (b) terrestrial vs. wetland patch use as indicated by the patch use index (PUI), and (c) terrestrial foraging efficiency indicated by the deer-squirrel index (DSI) through time for both upland (red) and floodplain (black) sites in the Middle Tennessee River Valley.

expected if resource depression were the cause. It is therefore unclear, based solely on relative abundance data, whether white-tailed deer were depressed in the MTRV or whether they simply appear less frequently in upland assemblages due to a general shift toward greater wetland patch use at this time (Figure 2; Table 3).

This patch choice explanation appears to be plausible given the currently available data, but it raises several questions that must be answered. First, the PUI suggests that a shift toward wetland patch use occurred in both upland and floodplain sites in the late Holocene. If this shift toward wetland hunting was the driver of the declining PD in upland sites, why then does PD not also decline in floodplain sites? This potential driver exists in both contexts, yet the PD only declines in the uplands. This discrepancy casts some doubt upon this explanation.

Second, assuming a shift in patch use from terrestrial habitats to wetlands drove the declining abundance of deer (PD) in late Holocene upland sites, why did this shift occur in the first place? The decision of when to switch patches is modeled by the marginal value theorem, which predicts that an individual should leave a

patch only when their foraging return rate in that patch drops to the average return rate across all available patches (Charnov 1976). Thus, a shift from terrestrial to wetland patch use should result from either declining foraging efficiency in the terrestrial patch or increasing foraging efficiency in the wetland patch.

Neither of these conditions appear to be met in the MTRV. Terrestrial foraging efficiency (the DSI) increases through time while, in a previous study, wetland foraging efficiency has been shown to have declined (Weitzel 2019). Therefore, it does not appear that hunting in wetland patches was incentivized by elevated wetland foraging efficiency in the late Holocene. Similarly, as the DSI remains high at this time, foraging return rates in terrestrial patches should have remained quite high.

It is possible that the models presented herein are missing more localized variation in foraging efficiency that could elucidate these relationships, however. For example, the DSI values from the upland site of Russell Cave show a decline in terrestrial foraging efficiency over the last 2,000 years (Table 2) that is not reflected in the regression model of upland foraging efficiency

Table 3. The general patterns in the three indices according to climate period.

Time Period	Date Range (cal BP)	Habitat	Proportion Deer (PD)	(Terrestrial) Patch-Use Index (PUI)	Deer-Squirrel Index (DSI)
Younger Dryas/ Early Holocene	12,900–11,750/ 11,750–8000	<i>Upland</i> <i>Floodplain</i>	Low Low	High Low	Low Low
Middle Holocene	8000–4000	<i>Upland</i> <i>Floodplain</i>	Increasing Increasing	Decreasing Increasing	Increasing Increasing
Late Holocene	4000–0	<i>Upland</i> <i>Floodplain</i>	Decreasing Stable	Decreasing Decreasing	Stable Increasing

(Figure 2c). Thus, perhaps terrestrial foraging efficiency did decline alongside deer abundance in localized cases. Declining returns in the terrestrial patch may therefore have led to a shift toward greater wetland patch use. Declining deer abundance could, in this case, be the cause of shifting patch use, instead of the consequence. It is also possible that in the late Holocene people at these sites were being drawn to wetland patches for reasons unrelated to caloric foraging efficiency, such as risk reduction foraging strategies, an Allee effect, or floodplain environmental modification. Whatever the causality may have been, this late Holocene shift in patch use currently poses more questions than it answers.

Therefore, additional work is necessary to determine whether white-tailed deer were depressed or not in the MTRV, and in eastern North America in general. Relative abundance data alone is insufficient in this case, but reports on faunal data from assemblages in the MTRV do not contain enough information to conduct additional analyses. Future research should investigate other zooarchaeological patterns using additional data and following the work of Wolverton et al. (2007, 2008, 2012). Wolverton (2008:Figure 2; Wolverton et al. 2008) provides a theoretical model of prey responses to hunting pressure which posits that deer populations under predation should be relatively juvenile-dominated and comprised of larger-bodied individuals. This is because predation increases mortality while fertility remains constant or potentially increases (Lyman 1987; Wolverton et al. 2008:5), and population reduction from predation results in less competition over resources with conspecifics, leading to larger body size (Wolverton et al. 2007). In contrast, a population under minimal or no predation should yield a faunal assemblage consisting of small- to medium-sized individuals, due to greater competition over limited resources, and a higher proportion of adults, due to lower mortality.

In addition to body size and age profiles, prey body part representation and bone fragmentation provide evidence on resource depression. Carcass processing efficiency can be measured by the average economic utility of prey body-parts processed and transported by humans (Metcalf and Jones 1988). Resource depression

can lead to an increase in mean part utility present at archaeological sites which were residential base camps. When local prey populations are depressed, hunters must travel further afield to hunt, and to mitigate the high cost of transporting complete deer carcasses, they may selectively butcher the carcass and return with only the highest-utility skeletal parts to maximize their economic efficiency (Broughton 2002; Cannon 2003; Nagaoka 2005).

As both increases and decreases in mean utility may indicate depression depending on local ecology, bone breakage can provide a useful additional line of evidence. The fragmentation of bones may increase when prey are depressed as hunters more intensively process carcasses to extract grease and marrow – sources of nutrients that are more costly to exploit than meat (Bar-Oz and Munro 2004; Morin and Soulier 2017; Munro 2004; Munro and Bar-Oz 2005; Nagaoka 2005). When taken together, these zooarchaeological measures would paint a more detailed picture of white-tailed deer depression (or a lack thereof) than the currently available abundance data are capable of providing.

Taphonomic considerations

As in any analysis employing data from multiple sites, the effects of taphonomy and recovery must be addressed. As noted above, faunal remains were recovered from 6-mm (1/4-in) screens at the upland sites of Russell Cave, Stanfield-Worley, and LaGrange shelter. At the floodplain sites of Dust Cave, Mussel Beach, and Widow's Creek, remains were recovered from 6-mm mesh as well, with additional flotation or feature samples screened through finer mesh. Recovery was therefore broadly consistent among the three upland sites and among the three floodplain sites, which are separately considered in these analyses, minimizing the impacts of recovery bias on these results.

However, the sites of Mussel Beach and Widow's Creek are open-air sites (albeit with shell midden contexts capable of good faunal preservation) while the rest are caves or rockshelters, likely with better preservation of faunal remains. This potentially impacts the floodplain model, as Dust Cave was occupied for the

first half of the temporal sequence considered here and these two open-air sites were occupied during the latter. It may therefore be that smaller fauna and lower-density elements are underrepresented in the late Holocene contexts of the floodplain models assessed here. This could contribute to the perceived abundance of deer relative to other taxa (the PD) or relative to squirrels (the DSI). If taphonomy biased these assemblages in this direction, it is possible that the indices evaluated here for floodplain sites are actually more similar to those of upland sites, and therefore that deer may not have increased in abundance so strongly, or perhaps at all, in late Holocene floodplain contexts. Additional work with data not currently available (e.g., assessments of skeletal element preservation and density-mediated attrition) is needed to investigate this potential complication.

Implications for regional archaeology

Whether or not white-tailed deer were depressed in pre-colonial North America has great bearing on archaeologists' understanding of numerous socioeconomic shifts. For example, debates concerning the origins of horticulture in eastern North America currently hinge on whether intensification drove the initial domestication of the crops of the Eastern Agricultural Complex ca. 5000 cal BP (see discussion in Weitzel 2019; Weitzel and Coddling 2016). One camp argues that domestication is driven by intensification – an increase in foraging yields (kilocalories per unit area) made possible by a decline in foraging efficiency (kilocalories per unit time) – propelled either by anthropogenic resource depression or environmentally driven reductions in high-efficiency prey types (e.g., Kennett and Winterhalder 2006; Winterhalder and Goland 1997). Others argue that it results from experimentation in times and places of resource richness and abundance with no intensification of subsistence (e.g., Smith 2016; Zeder 2012, 2015).

White-tailed deer in eastern North America play a large role in this debate because, as the highest-ranking prey type commonly exploited in the region, their abundance speaks to the state of the Native subsistence economy on the eve of domestication, whether intensified or not. Smith (2011, 2012, 2015) argues that there is no evidence for reduced foraging efficiency and intensification, whether induced by resource depression or environmental change, prior to initial domestication. To support his claim, he cites qualitative faunal data indicating that deer remains were abundant at the earliest sites with evidence of domestication (Smith 2011; Smith and Yarnell 2009:6565). In

an analysis of faunal assemblages from the same six sites in the MTRV analyzed herein, Weitzel (2019) also found abundant white-tailed deer, and no evidence for declining terrestrial foraging efficiency prior to initial domestication. However, he did find evidence for a decline in wetland patch foraging efficiency prior to initial domestication, which is consistent with the intensification hypothesis of domestication. Combined with environmental shifts associated with the Hypsithermal climate period (Weitzel 2019:203–205) and increasing human populations in the region (Weitzel et al. *in press*; Weitzel and Coddling 2016), data from the MTRV are consistent with the hypothesis that subsistence intensification, at least in certain habitats, drove initial domestication. While white-tailed deer may have been increasingly abundant on the landscape of eastern North America at the time of initial domestication, this does not mean that intensification did not occur for other taxa in other patch types.

The question of deer depression also impacts our understanding of the scale of much later colonial period impacts of Euro-American colonization. In western North America, depressed mule deer populations rebounded following European colonization (Fisher 2018; Jones 2016). Such environmental rebound may have led to the widespread accounts of European colonists who wrote of bountiful wildlife upon arriving in uncolonized locations (Broughton 1994a:371–372; Denevan 2016). Equivalent rebound has yet to be documented archaeologically in eastern North America, but it would not be expected if white-tailed deer were never depressed in precolonial times in the first place.

Other colonial period changes in deer abundance have been noted in eastern North America in the context of the deerskin trade (Carlos and Lewis 2010; Kardulias 1990). In southeastern North America deerskin dominated the fur trade, extending from the early seventeenth through the nineteenth century with peak intensity around the mid-eighteenth century (Braund 1996; Kardulias 1990; Lapham 2004, 2005, 2017; Pavao-Zuckerman 2007; Waselkov 1989). Lapham (2004, 2005:79–87, 2017) argues that the deerskin trade led Native hunters in seventeenth-century Virginia to selectively target prime adult males all year-round, a pattern that is also identified at other sites in the region. Cutmarks on deer bones consistent with skinning and tools used in hide preparation such as beamers (for scraping hair and tissues from hides) also become more common as a result of the deerskin trade (Lapham 2005:88–101). This intensification of deer hunting in the colonial period may have further

depressed deer populations if they were already depressed or depressed them for the first time if they were not previously.

Landscape burning and deer

As discussed previously, it is possible that white-tailed deer were not depressed in the MTRV (at least in floodplain settings) due to facilitation by humans in the form of environmental modification. It is now understood that precolonial North America was not a pristine wilderness (Denevan 1992, 2011), but that Native peoples had altered their environments for millennia. This alteration typically occurred in the form of burning: foragers and farmers alike would set fires to clear land for horticulture, remove understory vegetation, and promote the abundance of certain plant and animal species (Abrams and Nowacki 2008; Cronon 1983; Gremillion 2015; Liebmann et al. 2016; Lightfoot et al. 2013; Patterson and Sassaman 1988).

In the region surrounding the MTRV, charcoal data from several pollen cores provide evidence for landscape burning by Indigenous people (Chapman et al. 1982; Delcourt 1979; Delcourt et al. 1983, 1986, 1998; Delcourt and Delcourt 1997, 1998). Data on charcoal concentrations and influx were downloaded from the Global Paleofire Working Group's Global Paleofire Database (Global Paleofire Working Group 2020; Power et al. 2010). I constructed age-depth models to assign calendar dates to each core using the **bchron** package (Parnell 2020), and details are available in Supplementary File 3. Together, six data-sets from the region (Figure 1) show an increase in the concentration and frequency of charcoal produced by fires in the late Holocene (Figure 3). At the sites of Horse Cove Bog, North Carolina (Figure 3a, b), and Cliff Palace Pond, Kentucky (Figure 3k, l), charcoal concentrations increase beginning ca. 4000 cal BP, along with charcoal influx at the latter site. Charcoal concentration and influx also increase after ca. 3000 cal BP at Cahaba Pond, Alabama (Figure 3e, f),

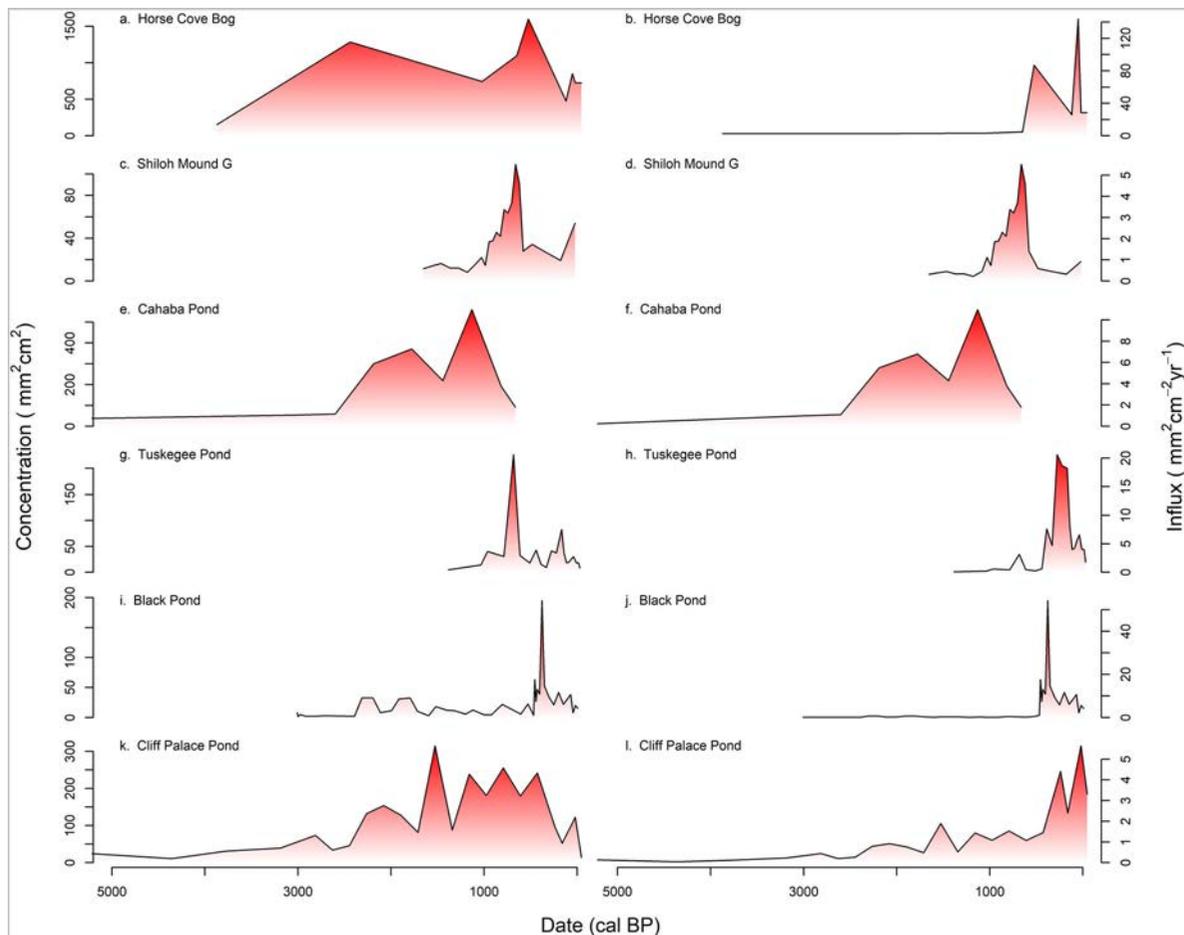


Figure 3. Charcoal concentrations and influx rates through time, as proxies for landscape fire, for six pollen core sites in the study region. Data were obtained from the Global Paleofire Working Group's Global Paleofire Database (Global Paleofire Working Group 2020; Power et al. 2010) and age-depth model details can be found in Supplementary File 3.

and after ca. 1500 cal BP at the Shiloh Mound site, Tennessee (Figure 3c, d). The data from Tuskegee Pond, Tennessee (Figure g, h), show increasing concentrations around ca. 1000 cal BP and high influx values after ca. 500 cal BP, likely due to burning by growing populations of Euro-American colonists. This same Euro-American signature is recorded at Black Pond, Tennessee (Figure 3i, j).

It may be no coincidence that the proportion of deer in upland assemblages began to decline while that of floodplain assemblages remained unchanged when landscape fires began to increase in the region surrounding the MTRV at the start of the late Holocene, between 3000 and 4000 cal BP (Figure 2a). As described above, white-tailed deer thrive in early successional habitats like those created by anthropogenic disturbance. It is therefore possible that landscape burning by humans facilitated white-tailed deer populations, increasing their numbers, or maintained deer populations under hunting pressure. If burning is a function of human population density, then it may have been more common on the floodplain of the MTRV than in the surrounding uplands given the higher population density in the former. Such a pattern may have facilitated deer populations in the floodplain, perhaps permitting a sort of garden-hunting (Linares 1976) if burning was for horticultural purposes, while human hunting in the relatively less-modified uplands depressed the species, resulting in the patterns observed in Figure 2a.

However, such a relationship cannot be demonstrated only from the data presented herein. It is commonly argued that floodplains were the primary locations of Native horticulture (Smith 1992, 2011). Thus, it might be expected that this could have facilitated deer populations in such locations and counteracted the depressive effects of larger human populations. Yet, others have argued that horticulture also occurred in uplands and was not unique to floodplains (Carmody 2014; Windingstad et al. 2008). Indeed, several of the pollen cores showing the earliest upticks in charcoal (Figure 3) come from the uplands (e.g., Horse Cove Bog and Cliff Palace Pond), confirming that upland populations also managed their landscape with fire, particularly in the context of horticulture (Gremillion 2015). Therefore, it cannot be reasonably concluded from these data that environmental modification facilitated white-tailed deer populations only in the floodplains and not the uplands. Declining deer abundance in upland but not floodplain sites may be the result of more prevalent landscape management in the floodplains relative to uplands, but such an inference is premature.

Additional work is necessary to investigate spatial heterogeneity in landscape fires and how such burning may have impacted deer populations.

Conclusion

The results presented here are equivocal on the question of white-tailed deer depression in the MTRV. White-tailed deer decline in abundance in upland sites after ca. 4000 cal BP, as would be predicted if they were depressed by growing human populations in the late Holocene. However, deer abundance does not decline in floodplain sites and the upland decline coincides with a shift toward greater wetland patch use and in the absence of clear declines in terrestrial foraging efficiency. It may be that deer were depressed in the uplands by human hunting but were facilitated in river valleys by anthropogenic environmental modification. However, the data presented herein are also consistent with the possibility that deer were never depressed in either upland or floodplain settings and that the decline in deer abundance in upland sites is due to a shift in patch use toward greater exploitation of wetland resources. This possibility raises additional unanswered questions, however, and skepticism is warranted. Overall, this study finds no clear evidence for resource depression of white-tailed deer in the MTRV. Additional evidence, in the form of more detailed zooarchaeological analyses of white-tailed deer bones, is needed to tease apart these potential causes and fully determine whether or not deer were depressed or facilitated in precolonial eastern North America.

Acknowledgments

Thank you to the Global Paleofire Working Group for making their database available, and to Natalie Munro and three anonymous reviewers for helpful comments and suggestions.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

The author received no funding related to this article.

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Data availability statement

All data and R code used herein are available as supplementary materials and are also archived at DOI 10.17605/OSF.IO/9ZV6C.

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