# White-tailed Deer Habitat-Use Patterns Across Forest Stands of Different Ages

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**Abstract** - *Odocoileus virginianus* (White-tailed Deer) overpopulation in eastern North America has largely been driven by an overabundance of optimal habitat, leading to numerous negative impacts on forest health and regeneration. Intermediate-aged forests are not highly preferred by White-tailed Deer, but preference shifts as forests age into mature stands because there is a greater amount of adequate plant species for White-tailed Deer to browse. We surveyed differences in wildlife habitat-use patterns in northeastern New York (Clinton County) in order to evaluate how White-tailed Deer differentially utilized 2 managed forest stands: (1) a mature forest (40 years post-harvest) and (2) an intermediate-aged forest (16 years post-clearcut). We monitored seasonal and diel wildlife habitat-use patterns using camera traps from March 2018 to September 2019. White-tailed Deer used the mature stand more often than the intermediate stand, particularly in the fall and spring, and shifted activity away from both stands in the winter. We suggest that stand-level forest management practices may be an effective way to manage the impacts of White-tailed Deer and maintain resilient forest ecosystems.

# Introduction

Landscape features heavily influence the way in which *Odocoileus virginianus* (Zimmerman) (White-tailed Deer) interact with the environment (Hurley et al. 2012, Johnson et al. 1995, Williams et al. 2011). Forest composition varies broadly from conifer- to deciduous-dominated, and successional stage, varying from young to mature, can influence the availability of food sources, hiding cover, and predator abundance (Campbell et al. 2004, Johnson et al. 1995, Lesage et al. 2002). Forest-land clearing for agricultural and/or timber use significantly changes successional trajectories, often resulting in optimal browsing conditions for White-tailed Deer, and facilitating shifts in home ranges and seasonal habitat usage (Côté et al. 2004, Horsley et al. 2003). Recently clearcut forests boast higher abundance of succulent woody browse (Côté et al. 2004, Tilghman 1989). Other benefits of recently cut forest include edge-effects, or boundaries between 2 or more habitats where open space is directly adjacent to effective cover, that provide White-tailed Deer with browse and shelter from predators (Williamson and Hirth 1985).

However, benefits from early successional forests are ephemeral, and as forests move into mid-successional stages (between ~10 and 40 years of age, hereafter referred to as intermediate), benefits diminish (Johnson et al. 1995). Thickets, resulting in mobility constraints and low food availability, may explain why White-tailed Deer do not use intermediate forests as often as mature forests. In contrast,

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mature forests are much more open, facilitating White-tailed Deer passage, and produce larger seed crops, especially during masting years (Johnson et al. 1995). Finally, mature forests contribute more to the diet of White-tailed Deer than intermediate forests primarily due to mast and fallen canopy fruits (Johnson et al. 1995). However, it has been found that habitat use varies by sex, with females on average using denser forests than males (Lesage et al. 2002) Predation risk can likely vary by successional stage as well (Doherty et al. 2022). Certain predators, such as ambush predators, benefit more from an intermediate or mature forest than early successional forest due to an abundance of cover. Other predators, such as pursuit predators, benefit more from open areas with low densities of vegetation.

Predator-prey habitat-use patterns may shift in space and time as a function of demographics, life stage, and life-history strategy reflecting avoidance among those most vulnerable (Clare et al. 2023). Cave et al. (2021) documented changes in overlap among Canis latrans Say (Coyote)-White-tailed Deer and Coyote-Lepus americanus Erxleben (Snowshoe Hare) relationships based on season. Coyotes tend to target Snowshoe Hares year-round, but show a higher probability of tracking White-tailed Deer in the spring when newborn fawns are unable to defend themselves as well as adults (Ballard et al. 1999). Higdon et al. (2019) provide additional support for the importance of monitoring fine-scale temporal wildlife habitat-use patterns as they noted diel activity of White-tailed Deer buck and doe align with that of Coyotes, peaking in the crepuscular hours. These same researchers observed predator-avoidance behaviors during the spring, with doe-fawn groups exhibiting diurnal activity peaks, thereby temporally separating from Coyotes. Crawford et al. (2021) noted similar diel-activity shifts (temporal refugia) among White-tailed Deer and Coyotes, during seasons of greatest predation risk, specifically spring parturition.

Differences in forest composition may also interact with seasonal changes (Barrett and Schmitz 2013) and predator-prey relationships (Doherty et al. 2022) to further influence variation in White-tailed Deer habitat usage (Beier and Mc-cullough 1990). White-tailed Deer may be more likely to congregate in dense confier forests in harsh winter conditions. Conifer forests provide habitat that offers insulating protection against snow and wind. Thick lower branches trap heat (Ozoga and Gysel 1972) and shield White-tailed Deer from extreme winter weather, facilitating energy conservation and thermal benefits (Mcgraw et al. 2022, Ozoga and Gysel 1972). *Juniperus virginiana* L. (Eastern Red Cedar) boughs are a relatively highly available and consumed winter food source, and while White-tailed Deer are not able to thrive off of Cedar alone, it is enough to sustain them for short periods of time (Swihart and Picone 1998).

Deciduous forests offer a different suite of benefits, which often includes greater access to preferred browse in the form of spring ephemerals (e.g., *Trillium grandiflorum* (Michx.) Salisb. [Northern White-flowered Trillium] and *Maianthemum canadense* Desf. [Canada Mayflower]) (Cale et al. 2013, Godefroid et al. 2005, Wakeland and Swihart 2009). As spring ephemerals wane, summer bud burst among woody plants results in a flush of high-quality food often less heavily defended and thus more palatable to White-tailed Deer (Stewart et al. 2011). Autumn seed crops are also greater in deciduous forests, especially during masting years. Tree species, such as *Fagus grandifolia* Ehrh. (American Beech) and *Quercus* spp. (oaks), go through multi-year cycles of masting during which they produce large amounts of seed providing dense caloric nutrients for White-tailed Deer (Cale et al. 2013, Harlow et al. 1975, McShea and Schwede 1993, Sork et al. 1993).

White-tailed Deer have become overabundant across eastern North America, resulting in the loss of ecosystem services and the need for local and regional management to ensure forest regeneration, prevention of invasive species spread, and long-term resiliency (Augustine and DeCalesta 2003, Averill et al. 2018, Côté et al. 2004, deCalesta and Stout 1997, Horsley et al. 2003, Lesser et al. 2019, Nagy et al. 2022, Rooney and Waller 2003, Russell et al. 2017). In particular, tree seedling regeneration has been severely impacted by overbrowsing in many areas (Côté et al. 2004, Rooney 2001, Tilghman 1989). Additionally, native spring ephemerals (e.g., Northern White-flowered Trillium, Canada Mayflower) have seen significant population decline as White-tailed Deer populations increase (Rooney 2001, Shelton et al. 2014). Overbrowsing also alters light levels, which further contributes to elimination of herbaceous species from the understory (Gill and Beardall 2001, Latham et al. 2005). Deer overabundance influences invasive species spread (Gorchov et al. 2021), soil nutrients, mycorrhizae abundance, and other wildlife populations (Rawinski 2008, Shelton et al. 2014). The long-term effects of Whitetailed Deer overabundance on forested ecosystems call for a better understanding of their habitat use, as well as the management efforts involved to regulate it.

Currently, the New York State Department of Environmental Conservation (NYSDEC) promotes hunting as the main strategy to regulate White-tailed Deer populations (NYSDEC 2012). However, given the increasing abundance of White-tailed Deer coupled with declining hunter numbers, this strategy is proving insufficient (Stedman et al. 2004, Winkler and Warnke 2013). There is a growing need for forest-management practices that promote forest health such as by limiting White-tailed Deer populations and shifting them elsewhere on the landscape (Sage et al. 2003). For example, promoting intermediate-aged forests in certain areas may encourage White-tailed Deer to disperse, thus limiting over-browsing.

We performed a camera-trap survey to determine White-tailed Deer habitat usage in 2 forest stands, at different successional stages, in the northeastern Adirondacks of New York. The primary objective of this study was to determine if White-tailed Deer were differentially using mature forest (no harvesting activity in ~40 years) versus an intermediate-aged forest (clearcut ~16 years ago, circa 2002). We hypothesized that White-tailed Deer would generally use the mature forest more than the intermediate forest given it should have a higher abundance of preferred food sources (Johnson et al. 1995) and lower predation risk due to lower stand density (Ballard et al. 1999, Higdon et al. 2019). Since White-tailed Deer tend to move to conifer stands in the winter for increased thermal cover and winter browse, we also hypothesized that White-tailed Deer would proportionally use both stands less in the winter (Cale et al. 2013, McGraw et al. 2022, Wakeland and Swihart 2009).

# Methods

# Study site

Our study sites were located in a northern hardwood forest on William H. Miner Agricultural Institute property in West Chazy, Clinton County, NY. The 2 stands, one harvested circa 2002 (intermediate) and the other unharvested for over 40 years (mature) were separated by <1 km (Fig. 1). Both sites were representative of northern hardwood forest with a mix of *Acer saccharum* Marshall (Sugar Maple), *Betula alleghaniensis* Britton (Yellow Birch), American Beech, *Populus deltoides* W. Bartram ex Marshall (Eastern Cottonwood), and low abundances of other common northern hardwood species (Fig. 2). These similarities facilitated direct comparisons of wildlife usage based on the management differences between the 2 stands, while holding all other environmental and location variables as constant as possible (Figs. 1, 2). The intermediate forest stand was ~100 ha in size nested within forest characteristic of our mature forest site (>1000 ha).

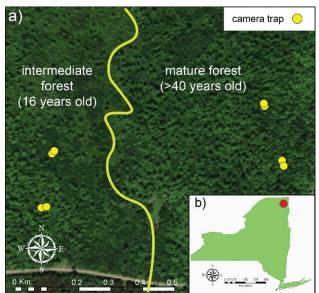
# **Field methods**

We placed 4 camera traps (Bushnell HD) in each stand in March 2018 to record wildlife occurrences. We strapped the cameras 0.5 m above the ground on tree trunks in order to capture smaller wildlife (e.g., *Pekania pennanti* (Erxleben) [Fisher] and Snowshoe Hare) occurrences along with larger animals (e.g., White-tailed Deer, Coyote) (Meek et al. 2014), which allowed us to analyze diurnal changes in predator–prey relationships. Within each stand, we positioned 2 cameras (Fig. 1) pointing in opposite directions to provide a comprehensive view of the site (Fig. 2). We set the cameras to capture photos based on motion detection every 10 sec.

# Wildlife-occurrence analyses

To assess wildlife usage in each stand, we sorted and analyzed the captured photographs using the 'camTrapR' package in R (Niedballa et al. 2018). To

Figure 1. (a) Map of experimental layout in the intermediate and mature northern hardwood forest in West Chazy, NY. Two camera traps were situated in each stand.(b) Regional location of study site within New York State.



ensure temporal independence between images of the same species on the same camera, we used a minimum delta time of 5 min. (Cave et al. 2021, Meek et al. 2014, Niedballa et al. 2018). While some studies have used times of up to 1 hour to avoid double-counting White-tailed Deer that linger at a camera site (Watts et al. 2008), other studies have found that shorter time periods are suitable (Kelly and Holub 2008, Meek et al. 2014). We processed camera data using delta values varying from 5 to 60 min. and compared results to determine that the 5-min. interval adequately captured all wildlife species, while not double-counting larger, lingering animals (Cave et al. 2021). All subsequent camera-trap analyses used these 5-min processed data.

To determine relative habitat usage, we calculated the number of individual occurrences per camera day for all observed wildlife species in each stand over the full course of the study (winter 2018 to summer 2019 inclusive). We used chi-square

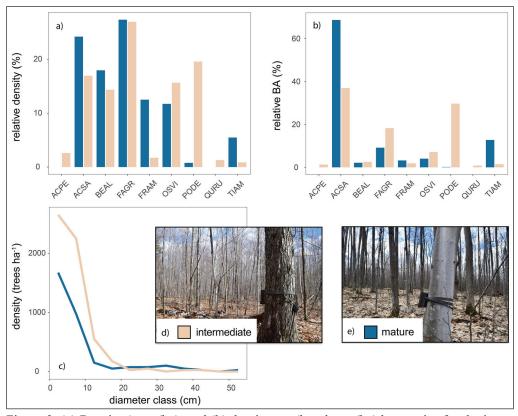


Figure 2. (a) Density (trees/ha), and (b) dominance (basal area/ha) by species for the intermediate and mature forest stands. Values are based on four 10 m x 10 m plots at each stand. (c) Structure of the intermediate and mature forest stands by number of trees in each 5-cm diameter class. (d–e). representative photographs of the 2 forest stands. Note the number of trees and size of trees in photos in relation to panels a–c. Also note the camera trap position near the base of the foreground tree in each photo. Species codes: ACPE = Striped Maple, ACSA = Sugar Maple, BEAL = Paper Birch, FAGR = American Beech, FRAM = White Ash, OSVI = American Hop-hornbeam, PODE = Eastern Cottonwood, QURU = Red Oak, TIAM = American Basswood.

tests to determine if differences in observed occurrences between the 2 stands were significantly different from the expectation that they were being used equally by species. Further, we calculated White-tailed Deer occurrences per camera day by season over the study period, and again used chi-square tests to determine if observed differences were significantly different from the expectation that they were being used equally. Finally, we used the activity kernel density estimation tool in 'camTrapR' (Niedballa et al. 2018) to examine diurnal activity patterns for White-tailed Deer and Coyotes, their primary natural predator in the region (Kilgo et al. 2010). We also examined diurnal patterns of Snowshoe Hare in relation to Coyote activity, to determine if Coyote behavior was affected by differing prey availability and/or stand-level activity.

## **Forest-composition analyses**

To quantify forest structure and composition in the 2 stands, we sampled four  $100\text{-m}^2$  plots/stand in late spring 2018. We tallied all woody stems >2.5 cm DBH by species and diameter within each of the plots. We then randomly located four  $1\text{-m}^2$  subplots within each main plot to sample understory vegetation. Within each subplot, we tallied all browsable units of herbaceous plants and woody seedlings (<1.3 m in height) by species in late spring 2018 and again in late spring 2019.

For the forest overstory and shrub data, we calculated relative tree density as the number of stems/ha and basal area as the cross-sectional area of all stems in  $m^2/ha$  by species for each stand. We also calculated the overall density across all species for each stand. We used student *t*-tests to determine if differences in density and basal area between the 2 stands were significant.

We calculated relative abundance as the proportional representation of each species in the plot of the herbaceous and woody understory for each stand in both 2018 and 2019 to determine the extent that understory vegetation differed between years. Further, we compared understory composition between intermediate and mature stands to evaluate any short-term changes in the understory vegetation due to White-tailed Deer browsing. We used non-metric multidimensional scaling within the R 'vegan' package (Oksanen et al. 2019) to compare understory relative abundance between stands and years. We also used student *t*-tests to determine if differences between years and sites were significant. All statistical analyses were conducted using R 4.2.2 (R core team 2022).

# Results

## Wildlife species occurrence

White-tailed Deer used the mature forest >2 times more than they used the intermediate forest (0.35 versus 0.15 occurrences per day, respectively; P < 0.001, df = 1, chi-square value = 46.4; Fig. 3), while Snowshoe Hare significantly favored the intermediate site (P < 0.001, df = 1, chi-square value = 11.84; Fig. 3). While Coyote slightly favored the mature site, there was no significant difference in occurrences (P = 0.37, df = 1, chi-square value = 0.81; Fig. 3).

Seasonally, White-tailed Deer usage varied widely, but followed the same overall pattern at both sites (Fig. 4). Based on chi-square tests, differences between sites were significant (P < 0.05) in both spring 2018 and 2019, fall 2018, and summer 2019, but not significant in either winter, or summer 2018 (Fig. 4, Table 1).

Figure 3. White-tailed Deer, Snowshoe Hare, and Coyote occurrences per day in the intermediate and mature forest stands over the study duration (winter 2018 to summer 2019 inclusive). "\*" or "ns" indicates significant or non-significant difference, respectively ( $P \le 0.05$  from chi-square test result) between stand types.

Figure 4. White-tailed Deer occurrences per day by season in the intermediate and mature forest stands. "\*" or "ns" indicates significant or non-significant difference, respectively ( $P \le 0.05$  from chi-square test result) between stand types.

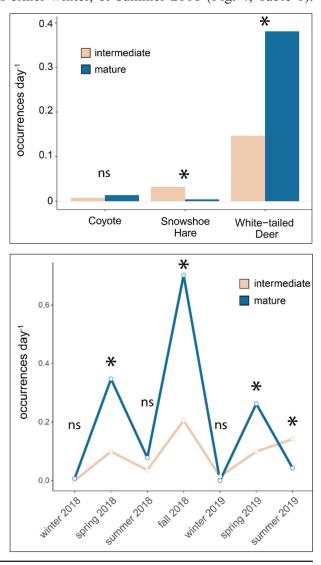


Table 1. Chi-square test results for comparisons of seasonal White-tailed Deer occurrences between the intermediate and mature forest stands. All tests used expected proportions of equal occurrences (50%) in each stand type compared to the observed occurrences.

Season	df	$\chi^2$	р
Winter 2018	1	1.00	0.317
Spring 2018	1	19.44	< 0.001
Summer 2018	1	2.25	0.134
Fall 2018	1	38.28	< 0.001
Winter 2019	1	2.00	0.157
Spring 2019	1	10.37	0.001
Summer 2019	1	7.54	0.006

A notable difference between the sites was the degree of change between seasons at the mature site being far greater than changes at the intermediate site (Fig. 4). Overall, White-tailed Deer usage was highest at both sites in spring and fall, with the maximum usage occurring in fall 2018 (Fig. 4). Winter usage was practically non-existent at both sites, while summer usage was also generally much lower than spring or fall (Fig. 4). Interestingly, summer 2019 was the only time over the 18 months of the study when White-tailed Deer were observed more often in the intermediate site than the mature site (Fig. 4).

Temporally, White-tailed Deer usage was highest at both sites during daylight hours but had pronounced peaks at dawn and dusk for the mature site, while being highest at midday for the intermediate site (Fig. 5). White-tailed Deer usage had much greater temporal overlap with Coyote usage at the mature site versus the intermediate site (0.67 versus 0.40, respectively; Fig. 5). At the intermediate site, where White-tailed Deer were not as common, Coyotes were most active overnight, with activity peaking just before dawn and in early evening—the same times as peak Snowshoe Hare activity (0.64 overlap). Conversely, at the mature site where Snowshoe Hare were relatively scarce (2 versus 17 occurrences), there was an increase in overlap between activity patterns of Coyotes and White-tailed Deer (Fig. 5).

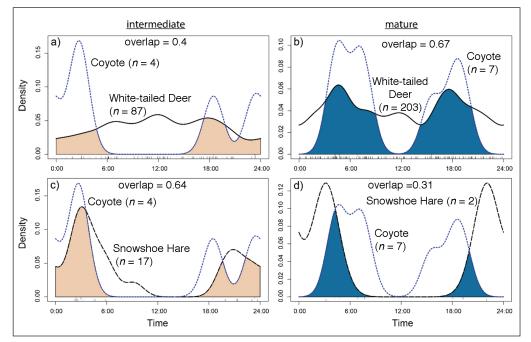


Figure 5. Activity plots comparing timing and usage between White-tailed Deer and Coyote in (a) the intermediate stand and (b) the mature stand, and Coyote and Snowshoe Hare in (c) the intermediate stand, and (d) the mature stand. Usage overlap is portrayed on each comparison as the shaded region and expressed as the percentage of shared area under the curves. Note differential occurrence (n) of species in each stand.

# Stand structure and composition

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The intermediate stand had a significantly higher density than the mature stand (5750 vs. 3200 trees/ha; P = 0.02, df = 6, t = 3.02). Basal area was also higher in the intermediate stand, but was not significantly different (40.1 vs. 32.4 m<sup>2</sup>/ha; P = 0.6, df = 6, t = 0.57). These differences were largely due to the high number of small-diameter stems in the intermediate stand (Fig. 2), as expected. Species contributions to basal area were relatively more evenly proportioned in the intermediate stand, while Sugar Maple dominated the mature stand (Fig. 2). Likewise, density was more evenly distributed among species in the intermediate stand compared to the mature stand. Species composition was similar between the 2 stands, with both containing Sugar Maple, Yellow Birch, American Beech, and Ostrya virginiana (Mill.) K. Koch (Hop-hornbeam). Major differences between the stands, however, were in the high abundance of Eastern Cottonwood in the intermediate stand and *Fraxinus americana* L. (White Ash) in the mature stand (Fig. 2).

Woody understory vegetation was dominated by Sugar Maple seedlings in both stands, but was significantly more abundant in 2018 than 2019 (P = 0.01, df = 6, t = 3.58; Fig. 6). Erythronium americanum Ker-Gawl. (Trout Lily), Wild Lily Of The Valley, and Aralia nudicaulis L. (Wild Sarsaparilla) were found in both stands (Figs. 6, 7). Additionally, other notable species found only in the mature stand included Trillium, Streptopus lanceolatus (Aiton) Reveal (Twisted Stalk), Uvularia perfoliata L. (Perfoliate Bellwort), and White Ash seedlings (Figs. 6, 7). Rawinski (2014) noted these woody and herbaceous species to be preferentially palatable browse. Non-metric multidimensional scaling clearly differentiated understory composition between the 2 stands and between years (Fig. 7). Stress and total variance associated with the ordination were 0.052 and 0.997, respectively.

## Discussion

Understanding White-tailed Deer usage of different-aged forest stands can help inform deer-management practices. Overall, our hypotheses were supported, with the intermediate stand being used far less than the mature stand. This finding is most likely due to the higher basal area and density in the intermediate stand decreasing both preferred browse availability and maneuverability (Johnson et al. 1995). However, it is important to note that our results are based on a small sample size with limited replication, and that additional, more comprehensive studies are needed to corroborate these findings. It is also worth noting that White-tailed Deer overabundance in the Adirondack region of upstate New York is much less severe compared to other regions of the state and the Northeast); however, White-tailed Deer are still overabundant compared to historic population levels and exert a significant impact on forest ecosystem structure, composition, and overall function (Lesser et al. 2019, Rooney 2001).

Intermediate and mature forests boast varying levels of nutritional value for White-tailed Deer. The intermediate stage has been shown to support an inadequate forage base compared to both early successional forest and mature forest (Johnson et al. 1995). Once the forest matures ( $\geq 40$  years), it becomes a significant producer of

high-nutrient nuts and fruits that White-tailed Deer tend to favor (Cleavitt and Fahey 2017), including those of American Beech, which had the highest relative density at our mature site. While White-tailed Deer actively avoid browsing on American Beech, as the leaves are difficult to eat and digest (Williamson and Hirth 1973), they do favor beechnuts which are only produced in large quantities on mature trees

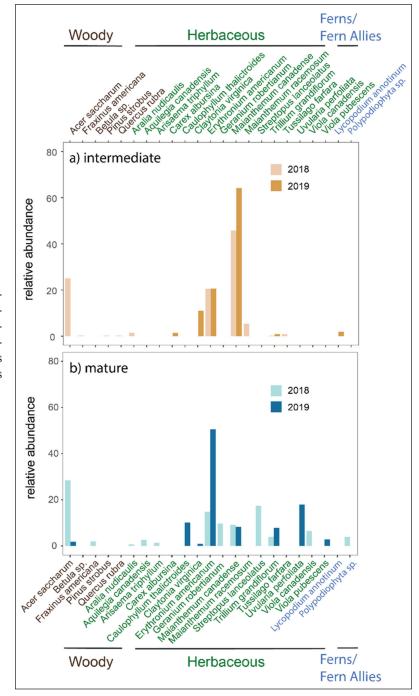


Figure 6. Understory composition for the intermediate and mature stands across the 2 study years (2018–2019).

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(Cleavitt et al. 2008, McNulty and Masters 2019). Conversely, younger American Beech (often present in dense thickets due to Beech bark disease) may have cascading detrimental effects on habitat quality (Cale et al. 2013, Cleavitt et al. 2008). Not only do White-tailed Deer not browse on the American Beech saplings themselves, but Cale et al. (2013) noted that as lignin-dense beech leaves decompose, conditions in the understory are less favorable towards herbaceous plant emergence, and that in sites that did not contain beech thickets, understory plant diversity was greater. Beech saplings also create low-light environments in which many species are unable to survive (Cleavitt et al. 2008). This appears to be the case at our intermediate site, where American Beech thickets were present and preferred browse species were far less common. White-tailed Deer show a high preference for Trillium (Anderson 1994, Koh et al. 1996), Twisted Stalk (Kraft et al. 2004), Perfoliate Bellwort (Koh et al. 1996), and White Ash seedlings (Morrissey et al. 2008), which were only found at our mature site. In our study, however, we must note that between-year differences in understory composition may be due to the exact timing of sampling related to differences in growing degree days and flowering time, with sampling having occurred 2 weeks earlier in spring 2019.

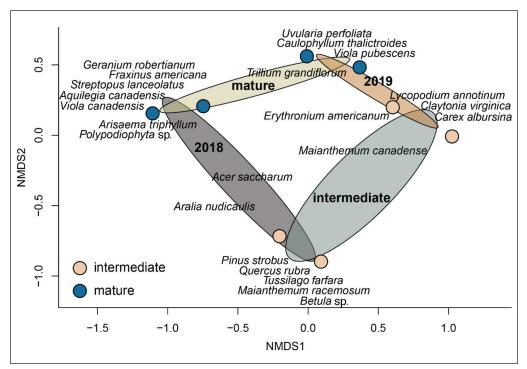


Figure 7. Ordination of understory composition by year (2018–2019) and stand (intermediate/mature) using non-metric multidimensional scaling. Text indicates understory drivers of year/site position (dots) in the ordination space. Ellipses indicate groupings of stands and years. The ordination summarizes community data (such as species composition data) by producing a low-dimensional ordination space in which similar sites are plotted close together based on the species composition and dissimilar sites and species are placed far apart.

In addition to variation in habitat usage based on available sustenance, Whitetailed Deer display seasonal shifts in habitat use due to changes in resource availability and quality, weather conditions, and predator presence (Beier and Mccullough 1990). However, our results showed that season had little effect on how White-tailed Deer used the 2 different-aged forests, with the mature stand being preferable in all seasons (with the exception of summer 2019). The magnitude of difference between seasons within stands changed seasonally, with White-tailed Deer occurrences in the mature stand being proportionally much higher in spring and fall than summer and winter. This result may be related to fall seed-crop availability (McNulty and Masters 2019), and spring ephemeral presence.

Winter occurrences at both sites were very low, suggesting that White-tailed Deer are seeking resources and shelter elsewhere—most likely in forest with a greater dominance of conifers. Demand for areas where deer congregate in winter is a function of cover and browse species, winter severity, and White-tailed Deer abundance across their range (Voigt et al. 1997). Conifers retain their leaves throughout the year and thus provide browse as well as protection against cold and harsh temperatures during winter (Delgiudice et al. 2006, McGraw et al. 2022, Ozoga and Gysel 1972).

In addition to low winter usage, summer usage was also low across both sites as well. This finding may be due to the changes in browse quality (e.g., protein, secondary metabolites) over the growing season (Dostaler et al. 2011) and that most of the favored stems and leaves have been browsed by summer (Johnson et al. 1995). With vegetation being heavily browsed prior to the summer months, White-tailed Deer have fewer available resources on which to feed, and shift to more profitable habitats (i.e., young or clearcut forests; (Williamson and Hirth 1985). Crawford (1982) noted that White-Tailed Deer in Maine change dietary composition seasonally with softwoods being of primary importance in the winter, shifting to forbs and hardwoods in spring and summer, and hardwoods and mushrooms into late fall. Browse choice often reflects availability and pairs with physiological need as the dietary items in late fall are more digestible than those in late summer, which helps deer obtain good physical condition ahead of the physiologically demanding winter season (Crawford 1982).

Predators also influence White-tailed Deer habitat-usage patterns, and their influence varies over time and space (Clare et al. 2023). In northern New York, Coyotes serve as an important apex predator, as *Ursus americanus* Pallas (Black Bear) are less common (Cave et al. 2011). Studies in the northeast and mid-Atlantic region have documented the role of Coyote predation as a key mortality factor regulating White-Tailed Deer populations (Ballard et al. 1999, Brundbridge 1993, Messier et al. 1986, Vreeland et al. 2010). White-tailed Deer often respond to Coyote presence by reducing foraging and increasing vigilance (Gulsby et al. 2018), contributing to varying seasonal and daily patterns of habitat use. Further, Coyotes tend to target fawns in the spring, causing a shift in both seasonal and daily movement (Crawford et al. 2021). In other words, daily habitat use between Coyote and White-tailed Deer might overlap more in the spring when fawns are vulnerable.

Other studies have shown White-tailed Deer to preferentially use denser growth and thickets (i.e., the intermediate-aged stand), during this timeframe (Crawford et al. 2021, Uresk et al. 1999). While we did not have enough data to assess seasonal shifts in Coyote habitat preference, we were able to determine that overall daily activity differed between the stands coinciding with Snowshoe Hare and Whitetailed Deer availability. We found that spring usage was proportionally the lowest of any season in the intermediate stand compared to the mature stand. These results suggest that predator abundance may not be high enough to influence prey behavior and habitat preference, but instead that predator dynamics are a function of prey availability.

In order to best manage for healthy forests, stakeholders must consider spatiotemporal shifts in wildlife habitat use on the basis of landscape-level contagion, stand age, season, and disturbance regime (Felix et al. 2007), in addition to predation risk (Clare et al. 2023, McShea 2012, Robinson et al. 2014). For instance, Barrett and Schmitz (2013) found that different silviculture strategies resulted in varied thermal effects on White-tailed Deer browsing. Intensive harvesting strategies tend to create warmer environments in the summer, and fluctuating environments in the fall. On the other hand, less-intense harvesting strategies lead to generally cooler and more variable conditions year-round, which show lower browse indices (Barrett and Schmitz 2013). Therefore, it's important to note how certain management policies might influence White-tailed Deer habitat use. Wildlife agencies have indicated a need to develop a White-tailed Deer management strategy that considers ecological relationships as well as habitat dynamics and distribution (Felix et al. 2007). Further, a single population of White-tailed Deer may occupy an area of a hundred to several thousand square kilometers (Voigt et al. 1997), which may therefore involve many different management strategies depending on landscape heterogeneity.

Studies, including our own, have shown that White-tailed Deer populations prefer mature forests for ideal browse (Johnson et al. 1995, Rooney 2001). As forests shift into intermediate age classes, suitability declines due to resource quality and structure, but then mature into more favorable habitat again (Johnson et al. 1995, Miller et al. 2009). Our results showed that White-tailed Deer preferred the mature forest and did not favor the intermediate forest. Therefore, maintaining a certain amount of forest in intermediate age classes may allow managers to focus Whitetailed Deer management efforts on specific parts of the landscape. Further, intensive silviculture practices (e.g., thinning, artificial regeneration) may prove more effective if managers allow forests to reach intermediate ages before implementation. Importantly, future studies need to determine at what point intermediate-aged forests transition back to being preferred White-tailed Deer habitat. Landscapelevel White-tailed Deer management, with consideration for habitat contagion and frequency of preferred habitat, is critical for achieving management objectives.

Finally, future research on White-tailed Deer habitat use needs to consider implementing studies across broader landscapes that capture (and replicate) stand type, legacy management practices, and stand age—all limitations in our study.

Additionally, it is important that adequate monitoring (i.e., number of cameras) is carried out within stands, and that monitoring protocols (i.e., camera placement) are standardized across sites and studies.

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