



A new rapid and efficient method to estimate browse impacts from twig age



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ABSTRACT

High densities of white-tailed deer restrict the regeneration of tree species, reduce understory cover and diversity, enhance invasions of exotic species, and facilitate the spread of human and deer diseases. Deer managers often base management decisions on estimated deer densities and carrying capacities, generating controversy. It may be simpler, cheaper, and more appropriate to manage deer populations in relation to their effects on local habitat conditions. Here, we describe a method based on the mean ages of woody twigs on saplings exposed to browsing. Growth can be traced back at least five years on deciduous species using terminal bud scale scars, generating estimates for the minimum interval between browsing events. We applied this method to three species of maple (*Acer*) growing in canopy gaps in- and outside a 5–7 year-old fenced deer enclosure in a mature forest in upper Michigan. Maples are palatable to deer but resprout readily after browsing. The method was simple and efficient to implement in the field with negligible among-observer variation. Mean twig age responded sensitively to differences in deer impacts among species, across the fence, and over time (all $p < 0.002$). *Acer rubrum* and *pensylvanicum* had lower mean twig ages than *A. saccharum* reflecting higher rates of browsing. Twig age showed a larger deer effect size and r^2 values than the sapling height or browse indicators (Cohen's $d = 34.85$ vs. 1.39 and 9.55 for height and browse; $r^2 = 0.556$ vs. 0.154 and 0.331). Twig ages declined with height outside the fence while rising inside, providing a second independent indicator of deer impacts. Twig ages provide a direct indicator of deer browse on regenerating trees with lower sampling variance and higher independence from local environmental conditions than height or browse incidence. We should next test the twig age method in other contexts and species to confirm that it is an efficient, sensitive, and reliable indicator of deer impacts and habitat conditions.

1. Introduction

Deer and elk selectively browse a variety of woody shrubs and trees and graze many herbaceous species. At higher densities, they eat more species and increasing fractions of the food available, indirectly favoring species that tolerate or avoid herbivory. At this point, ungulates act as a keystone herbivore to alter community structure and the distribution and abundance of many species (McShea and Rappole, 1992; Waller and Alverson, 1997; Augustine and DeCalesta, 2003; Côté et al., 2004; Goetsch et al., 2011). Cascading effects of ungulate browsing include the suppression of tree growth (Lucas et al., 2013), altered populations of small mammals (deCalesta, 1994) and birds (DeCalestra, 1994; Allombert et al., 2005; Cardinal et al., 2012), faster soil nutrient cycling (Gass and Binkley, 2011), and accelerated invasions of exotic earthworms and weedy plants (Williams and Ward, 2006; Eschtruth and Battles, 2009; Knight et al., 2009; Davalos et al., 2015; Dobson and Blossey, 2015). In eastern North America, high white-tailed deer

populations have limited rates of sapling recruitment enough to alter forest type and composition across broad regions (Bradshaw and Waller, 2016). High deer densities have also facilitated increases in disease load by facilitating the spread of Chronic Wasting Disease (Storm et al., 2013) and boosting populations of the ticks that spread Lyme and other tick-borne human diseases (Wilson et al., 1985; Deblinger et al., 1993; Kilpatrick et al., 2014).

Despite the number, severity, and significance of ungulate (deer henceforth) effects, few programs exist to monitor these in a systematic and continuing way (Morellet et al., 2007). This prevents most deer managers from basing their decisions on the magnitude of these effects. Instead, deer populations are usually managed to favor hunting and viewing opportunities using estimated deer densities to steer management relative to perceived biological and/or social carrying capacities. The uncertainties inherent in these estimates have added to the controversies surrounding deer management. Estimating deer densities is technically demanding, requiring extensive field sampling (e.g., scat-

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group count data) or elaborate population models. Models like the Sex-Age-Kill model used in several states depend on accurate records of hunter kills plus measures or assumptions for several key variables (Millsbaugh et al., 2009). In practice, estimating deer densities has proved to be costly, imprecise, and most reliable at large spatial scales. However, even if estimating deer densities were cheap and accurate, these densities would not necessarily tell us whether the deer herd could be supported by current habitat conditions or the trajectory of habitat conditions at each site.

Assessing habitat conditions is usually simpler, cheaper, and more accurate than first estimating deer density and then using that estimate to manage the deer herd. This means that having standard methods to monitor habitat conditions could give forest and wildlife managers a valuable tool for assessing the capacity of the land to sustain local deer populations. Having local data on habitat conditions would also match trends in many states to manage deer at more local levels. These data will also gain value once methods are standardized and applied across broader regions and successive years. These broad spatial and temporal data, in turn, would facilitate more comprehensive studies of regional differences and trends.

Here, we introduce a streamlined method for estimating deer impacts and habitat conditions by estimating the number of years that twigs can grow unmolested before being browsed (an inverse measure of the browsing rate). We first present the rationale for this measure and its basic design. We then describe how it is applied in the field and how the data it generates can be analyzed to infer browsing impacts. We test the method's sensitivity by comparing results from saplings in- and outside a fenced enclosure and among three species of maple (*Acer*). We also compare the power of twig age measures relative to two alternative measures – sapling height and the incidence of fresh browsing. We also explore relationships between twig ages and sapling height to test the hypothesis that taller saplings experience greater rates of browsing in the presence of deer. We conclude that this method has considerable promise and deserves to be tested in other species and locales. If its promise is borne out, the twig age method could be used to construct a network to efficiently monitor deer habitat conditions.

2. Motivation and rationale

The impacts that herbivores have on tree seedlings and saplings (henceforth saplings) reflect a race between growth and herbivory. Both are measured as rates or, inversely, as time intervals. When deer are dense, tree saplings have shorter intervals in which to grow before experiencing another bout of browsing that acts to limit growth. When deer are sparse, these intervals are long, allowing sapling growth to balance losses from other sources (insect herbivory, diseases, and attrition due to falling debris). This balance implies that faster growing saplings can tolerate higher rates of browsing while saplings growing slowly (due to either shade or a conservative growth strategy) may suffer more from herbivory. Thus, saplings growing under sunnier conditions generally tolerate more browsing. Conversely, slow-growing seedlings and saplings of shade-tolerant conifers like *Tsuga canadensis* and *Thuja occidentalis* that can spend decades in the “molar zone” are highly susceptible to even intermittent browsing. For deer-palatable species that already occur sparsely under shady conditions, browsing can further reduce their densities to such low levels that recruitment is effectively curtailed (Bradshaw and Waller, 2016).

Several methods exist to assess deer impacts on forest vegetation. None has yet emerged as a standard despite the value of having measures that could be compared over time and among sites. The species used to assess browsing should be widespread and of intermediate palatability because species that are highly palatable disappear quickly once deer populations increase while species avoided by deer provide no signal of deer effects (except perhaps by increasing in relative abundance). Herbaceous species that have been used to indicate deer impacts include *Trillium* (Rooney and Gross, 2003; Jenkins et al., 2007),

Clintonia (Balgooyen and Waller, 1995), *Chelone* (Williams et al., 2000), and other species (Webster et al., 2001). Such species may disappear, however, with more herbivory. In addition, their abundance or condition can reflect plant as well as deer density (Augustine et al., 1998) or may vary among communities (Frerker et al., 2013). This makes it difficult to use herbaceous plant species as standard indicators.

Woody species provide advantages as indicators of deer impact. First, they retain a woody structure that can be observed and measured even as they are browsed to the point of death. Second, woody seedlings and saplings often persist across a range of sizes, tolerating some deer herbivory while retaining evidence of these impacts. Third, canopy trees provide long-lived seed sources that provide a continuous rain of seeds even if seedlings continue to disappear due to browsing. To estimate rates of deer browsing, Frelich and Lorimer (1985) introduced a method based on enumerating the freshly browsed fraction of terminal twigs in sugar maple (*Acer saccharum*) located in the browsing zone. Several studies in the upper Midwest have used this method, but we have found it suffers from high sampling variance (reflecting the patchiness of deer browsing) and estimates often vary among observers. It therefore seems best suited for assessing large differences among sites. Morellet et al. (2001, 2003, 2007) introduced a simpler method that relies on surveying any and all woody seedlings and saplings already present, scoring these simply as having browsable twigs present at points along a transect and which of those show any sign of browsing. Such simple scoring avoids having to identify species or estimate browsing rates within stems affording statistical advantages provided sample sizes are large enough to dampen sampling variance reflecting patchy consumption. Rawinski (2016) proposed another method that also uses extant plants by measuring the height of the ten tallest saplings of particular tree species found within a plot. Blossey et al. (2017) proposed propagating and planting hundreds of red oak seedlings as sentinels to assess deer impacts. Their approach has advantages including using a standardized food source and being able to assess deer effects even at locations where deer have eliminated natural seedlings. However, it also requires advance efforts to locate sites and propagate and plant seedlings that must then be relocated and tracked in successive years. All these methods have merit and deserve to be directly compared to evaluate which are most reliable and informative.

Most efforts to estimate browse impacts on woody species measure one of three things: a) vegetative condition of the sapling or shrub (cover, height, density, etc.), b) reproductive condition (the number or frequency of flowers and fruits), or the incidence or fraction of browsed twigs. An interesting exception to these are methods that use plant architecture to infer browsing in western rangelands (Keigley and Frisina, 1998; Keigley et al., 2003). Because their method is mostly qualitative, we do not discuss it further. Woody plant cover, height, and density, however, all vary greatly in response to local differences in seed rain, seed bed conditions, soil nutrients, and light levels which also greatly affect flowering and fruiting. Estimating the current incidence of browsing avoids these problems, but patchy deer browsing and variation among observers inflate sampling variance. The twig age method reduces these sources of environmental variation by instead estimating the intervals between episodes of deer herbivory. As noted above, measuring the rate instead of the amount of herbivory addresses the key process of interest: the race between growth and consumption. Twig growth may be fast or slow, depending on both the species being observed and its local environment, but what matters is whether twigs are growing faster than they are being removed. Mean twig longevity also averages over 2–3 stems and up to 5 years of growth, further reducing sampling variance.

It would be difficult and time-consuming to quantify rates of twig growth by marking individual plants and measuring annual extension growth on their many twigs. It would be similarly laborious to measure intervals between deer consumption directly (e.g., by regularly revisiting marked twigs to record intermittent events of herbivory). Such measures are unnecessary, however, if the key variable of interest is

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