

The Kinzua Quality Deer Cooperative: Balancing White-tailed Deer Populations and Their Browsing Impact to Forests over Two Decades of Local Land Stewardship

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Abstract

The Kinzua Quality Deer Cooperative (KQDC) was established in 2000 to determine whether coordinated management of forest habitat and white-tailed deer (*Odocoileus virginianus*) populations in northwestern Pennsylvania could improve forest ecosystem health and deer herd attributes. Across a 30,000 ha project area, the KQDC monitored how deer populations, browsing pressure, and understory plant diversity and abundance responded to vigorous adaptive hunting pressure made possible through additional antlerless tags, concurrent hunting seasons, and sustained hunter engagement. The approach was largely successful. Deer densities were quickly reduced by 50 percent and then sustained for much of the 21-year period. Concomitantly, browsing impact on woody regeneration decreased while tree regeneration became more frequent throughout the study area. Despite these successes, deer densities rebounded in the past 5 years, partly due to withdrawing hunter incentives and reducing tag limits in State-level harvest regulations. These increasing deer populations and resulting intensified browsing pressure threaten to negate the gains made in habitat and herd health.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) population densities are currently at or above precolonial estimates of 4 to 8 deer per sq. km throughout much of the 110 million ha of forest land in the eastern United States (Hanberry and Hanberry 2020, McCabe and McCabe 1997). The consumptive and nonconsumptive impacts of high-density deer herds often diminish plant richness and abundance, degrade habitat, disrupt forest management, and hasten the spread of native and exotic plant invaders (Bernes et al. 2018). In Pennsylvania, high deer densities throughout much of the 20th century drastically altered forest understory vegetation composition and impeded sustainable forest management (Royo and Stout 2019). By the late 1960s, intense browsing influence over forest regeneration was so pervasive that even-aged regeneration harvests failed to regenerate trees. Instead, forest land shifted to fern- and herb-dominated areas. Where tree regeneration occurred, it was often dominated by the few species least susceptible to browsing, such as black cherry (*Prunus serotina*) and American beech (*Fagus grandifolia*) (Horsley et al. 2003). Thus, by the turn of the 21st century, forest managers routinely fenced regeneration harvests to exclude white-tailed deer, at considerable expense,

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to successfully regenerate diverse forests that would sustain a broad suite of ecosystem function and services.

In 2000, a group of private landowners, public land managers, scientists, hunters, and others, with the support and guidance of the Sand County Foundation (SCF), came together to form the 30,000 ha Kinzua Quality Deer Cooperative (KQDC) in northwestern Pennsylvania. The KQDC leadership team leveraged new regulations and deer management programs available through the Pennsylvania Game Commission (hereafter, Game Commission), coordinated Game Commission programs for managing habitat and deer, and developed outreach efforts. The goal of these actions was to improve habitat quality, enhance deer herd attributes, and sustain hunter engagement. To assess potential changes in habitat quality in response to lowered deer herds, the team used an extensive monitoring program to track changes in deer density, woody regeneration abundance, and browsing pressure. The KQDC capitalized on novel programs offered by the Game Commission, including concurrent antlerless and antlered deer seasons and the Deer Management Assistance Program (DMAP), which is a program that allowed landowners to request and distribute additional antlerless tags to focus hunting on specific land areas (Rosenberry et al. 2009).

In this study, we examine woody understory plant species responses to reduced white-tailed deer densities. We tested the hypothesis that reductions in deer populations will decrease overall browsing pressure on woody regeneration, thereby allowing woody regeneration to become more abundant across broad spatial and temporal scales. We further examined whether any reductions in browse pressure or gains in seedling abundance were eroded over the past 5 years as deer densities rebounded in response to lower hunting pressure resulting, in part, from a relaxation of game management policies.

METHODS

The KQDC is located within the unglaciated Allegheny High Plateau section of the Appalachian Plateau Province in northwest Pennsylvania, and has an average elevation of 613 m (range: 494 to 689 m; McNab and Avers 1994). Forests in this region are generally second-growth Allegheny hardwood, northern hardwood, and mixed oak stands that regenerated following the turn of the century exploitative harvests (Royo et al. 2021). Major species include black cherry, American beech, sugar maple (*Acer saccharum*), red maple (*A. rubrum*), black birch (*Betula lenta*), yellow birch (*B. alleghaniensis*), striped maple (*A. pensylvanicum*), white ash (*Fraxinus americana*), hemlock (*Tsuga canadensis*), and northern red oak (*Quercus rubra*).

In 2000, we randomly selected 26 blocks, measuring 259 ha (1610 m × 1610 m) each, within the 30,000 ha KQDC landscape as focal areas for data collection efforts. Beginning in 2002, we estimated deer densities yearly within each block following the fecal pellet group count method described by deCalesta (2013). Pellet group estimation methods can be inexpensively deployed across large landscapes and provide a measure of relative deer abundance (Forsyth et al. 2022). Briefly, the deCalesta (2013) method utilizes five 1,610 m long transects spaced 300 m apart to span the entire 259 ha block. Along each transect, observers count the number of pellet groups containing 10 or more fecal pellets in 1.2 m radius plots spaced at 30 m intervals. When adjusted for mortality, these surveys provide a relative estimate of deer densities present in the spring of that year.

In tandem with the pellet surveys, we estimated woody regeneration abundance and browsing impact in alternating plots along the transect (i.e., every 60 m). These surveys assess whether any tree regeneration exists on the plots and determine the frequency of occurrence (i.e., proportion of plots) and browsing intensity on six woody species: red maple, black cherry, American beech, striped maple, hemlock, and birch species. Vegetation surveys began in 2002, and birch (black and yellow, combined) was integrated into the protocol beginning in 2005. Following protocols established by Pierson and deCalesta (2015), we assessed browsing on individual stems 15 cm tall or taller but less than 1.8 m. The height range ensures that stems are accessible to white-tailed deer (Waller and Alverson 1997). Browsing impact is scored categorically, by species, as: zero (0 percent of stems browsed); low (1 to 50 percent of stems browsed); moderate (more than 50 percent of stems browsed); heavy (more than 50 percent of stems browsed and saplings were hedged); severe (more than 50 percent of stems browsed and saplings were hedged; less than 15 cm in height). For the purposes of this paper and ease of interpretation, zero and low were collapsed into a “Low” category and heavy and severe were collapsed into a “High” category.

We examined how overall tree regeneration abundance (i.e., proportion of plots containing regeneration of any tree species) varied in response to changes in deer densities across the 21-year period. Additionally, we tracked how abundance (i.e., frequency) and browsing intensity varied for each of the five focal species that we observed during all 21 years. We used repeated measures analyses of variance (ANOVAs) in a randomized complete block structure. Values for the block-level analyses used the mean value for each metric calculated from the five transects within a block. For analyses on deer density, overall stocking, and browse impact, year was considered as a fixed treatment variable and block was considered as a random variable. Analysis of individual species (browsing impact, frequency) included year, species, and year \times species as fixed variables and added species (block) as a second random variable. Deer density, browsing intensity and impact, and overall stocking were modeled using a normal distribution. Abundance of the core species was modeled using a lognormal distribution. The distribution of each variable was assessed prior to analyses, and we further examined homoscedasticity and normality of the residuals using boxplots and Levene’s test to ensure we met ANOVA assumptions. Correlations between years were modeled using an autoregressive first order covariance structure amended to the heterogeneous extension of the autoregressive first-order structure when necessary to adjust for heterogeneous residuals among years. When significant year effects were found, we simplified interpretation using contrasts to examine significant differences among three distinct deer management eras rather than look at pairwise differences among all 21 years (i.e., 210 comparisons). These eras were classified as before DMAP (pre-DMAP; 2002 through 2004), when harvest regulations were in the process of being implemented and hunting pressure intensified; DMAP (2005 through 2017), when regulations were sustained; and relaxed DMAP (2018 through 2022), when a combination of lowered harvest allocations, fewer DMAP tags, and abbreviated concurrent seasons combined to reduce hunting pressure on the landscape.

RESULTS

Deer populations averaged 10.4 deer per sq. km in the pre-DMAP era and then dropped by half to 5.2 deer per sq. km in the DMAP era. When harvest regulations loosened, deer

densities increased to an average of 8.3 deer per sq. km in the relaxed DMAP era (Fig. 1). As deer densities dropped, woody regeneration frequency steadily increased from 39 percent in the pre-DMAP era to 48 percent in the DMAP era and almost 54 percent in the relaxed DMAP era (Table 1). American beech was the most frequently encountered species, and its abundance increased by about 30 percent in the DMAP era before leveling off. Striped maple, the second most frequent species at the onset of the study, remained static over time. Black cherry nearly doubled in abundance in the DMAP era only to decline during the relaxed DMAP era to levels observed at the beginning of the study. Red maple steadily increased in frequency throughout the course of the study, from 3 percent of plots in the pre-DMAP era to nearly 16 percent in the relaxed DMAP era, becoming the second most abundant of the five tracked species. Finally, hemlock, the rarest species (fewer than 1 percent of plots), increased following reduction in deer densities in the DMAP era before leveling off.

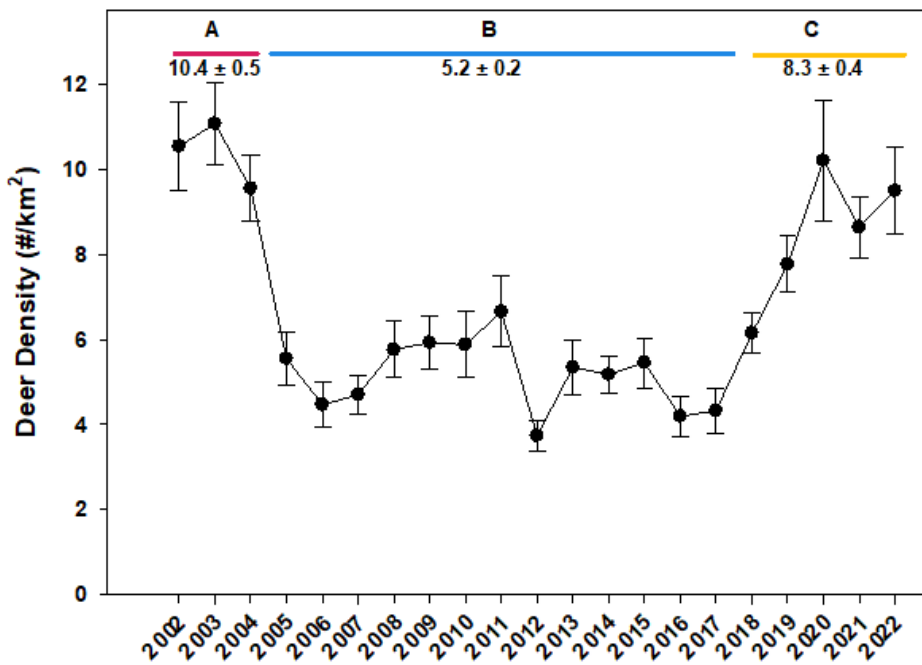


Figure 1.—Estimated deer densities (deer per sq. km) across the 21-year project period as assessed by springtime fecal pellet surveys, Pennsylvania. Error bars indicate ± 1 standard error around the estimate. Years are grouped into three distinct deer management eras and indicated by the horizontal lines at the top of the graph. The pre-Deer Management Assistance Program (DMAP) era (2002–2004), prior to the institution of enhanced doe permit availability and concurrent antlered and antlerless harvest, is labeled A. The DMAP era (2005–2017), when game management policies were in place, is labeled B. The relaxed DMAP era (2018–2022), during which extra doe permits were available, is labeled C. Values under the horizontal lines indicate average deer densities for each era.

Table 1.—Average woody regeneration frequency \pm 1 standard error throughout the Kinzua Quality Deer Cooperative landscape in northwestern Pennsylvania, as assessed by springtime browse impact surveys. Yearly data are summarized as the averages of each of three deer management eras: pre-Deer Management Assistance Program (DMAP) era (2002–2004), the DMAP era (2005–2017), and relaxed DMAP era (2018–2022). Different lowercase letters denote significant differences among the three eras.

Species	Pre-DMAP	DMAP	Relaxed DMAP
Any regeneration	39.3% \pm 1.7% a	48.4% \pm 0.8% b	53.6% \pm 1.1% c
American beech	16.9% \pm 1.5% a	22.2% \pm 0.6% b	23.8% \pm 1.0% b
Striped maple	7.5% \pm 0.9%	9.0% \pm 0.4%	7.4% \pm 0.5%
Black cherry	3.4% \pm 0.5% a	5.9% \pm 0.3% b	3.5% \pm 0.6% a
Red maple	3.0% \pm 0.6% a	10.5% \pm 0.7% b	15.9% \pm 1.2% c
Hemlock	0.6% \pm 0.1% a	2.1% \pm 0.2% b	2.2% \pm 0.2% b
Birch species	Not measured	7.8% \pm 0.4% a	10.4% \pm 0.6% b

■ High
■ Medium
■ Low

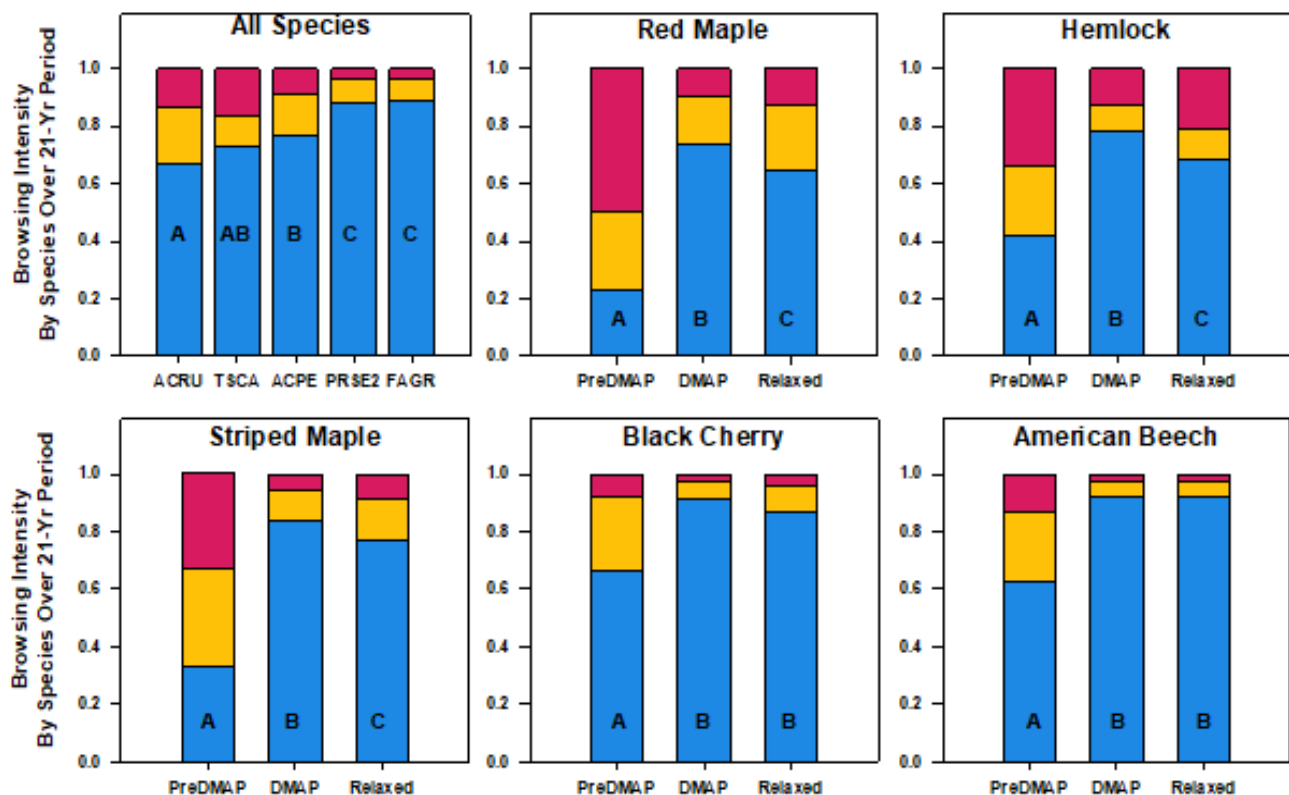


Figure 2.—Average browsing intensity throughout the Kinzua Quality Deer Cooperative landscape, Pennsylvania, as assessed by the springtime surveys for each Deer Management Assistance Program (DMAP) era, for all species combined and each of five focal species: red maple (ACRU), hemlock (TSCA), striped maple (ACPE), black cherry (PRSE2), and American beech (FAGR). Browsing is summarized by category: Low is 50 percent or fewer stems browsed; Medium is more than 50 percent stems browsed but seedlings are not hedged; and High is more than 50 percent of stems browsed and browsing has prevented growth into sapling size class. Yearly data are summarized as the average in each of three deer management eras: pre-DMAP era (2002–2004), DMAP era (2005–2017), and relaxed DMAP era (2018–2022). Different uppercase letters on bars denote significantly different browse susceptibilities.

The focal tree species differed in browse susceptibility (intensity) when averaged across the 21-year period (Fig. 2). Red maple and hemlock were the species most susceptible to browsing, striped maple had intermediate susceptibility, and black cherry and beech were the least susceptible species (Fig. 2). When examined individually, browsing pressure on every species declined in the DMAP era. The proportion of plots rated as experiencing low browse pressure increased by between 37 percent (black cherry) and 215 percent (red maple) in the DMAP era relative to the pre-DMAP era (Fig. 2). However, as deer densities rebounded in the relaxed DMAP era, browsing pressure increased on red maple, hemlock, and striped maple (Fig. 2).

DISCUSSION

Over 21 years, deer populations within the KQDC have waned and waxed as deer management policies changed. Beginning in 2000, the Game Commission enacted a series of policy changes that caused a rapid and substantial reduction in deer populations statewide. These changes, including the availability of additional doe tags through the DMAP and the 2-week concurrent season, concentrated hunting pressure on antlerless deer (Rosenberry et al. 2009, Wildlife Management Institute 2010). As deer densities and associated browsing pressure declined within the KQDC project area, woody regeneration of various focal species, as well as regeneration overall, became more abundant across the landscape. Thus, this study demonstrates that reducing deer population over time to levels within the historical range of variation (4 to 8 deer per sq. km; Hanberry and Hanberry 2020), enables forest understory recovery. These results extend findings from small-scale enclosure experiments that similarly find elimination of browsing pressure enhances tree regeneration (reviewed by Bernes et al. 2018). Other studies document that woody regeneration rapidly responds positively to reductions in browse pressure relative to other plant life forms (Habeck and Schultz 2015). This differentiation occurs as reproductive individuals remain on-site and can continue to supply propagules that fuel recruitment, whereas herbaceous layer species are often locally extirpated or at low abundance (Habeck and Schultz 2015).

Our monitoring protocols determined that the five focal taxa separated into three palatability bins. We found red maple and hemlock, species reported as moderately to highly preferred or intolerant to browsing, or both (Frelich and Lorimer 1985, Lesser et al. 2019), were most likely to suffer browsing, and both increased in abundance (i.e., frequency) as deer populations declined in the DMAP era. In contrast, our monitoring efforts ranked black cherry and American beech as least susceptible to browsing, corroborating findings by other researchers (Champagne et al. 2021, Healy 1971). Although our rapid browsing assessment is less detailed than other published methods (Morellet et al. 2001, Potvin 1995, Waller et al. 2017), it proved remarkably accurate in discerning palatability rankings among species. Such coherence with relatively low-resolution data is likely possible through the use of long-term records collected across large areas scaled to the average home range size of white-tailed deer (e.g., Tierson et al. 1985). This aggregate approach likely reduces the high temporal and spatial variation often observed in browse impact surveys; the observed variation may be attributable to shifts in deer populations and forage composition and availability, among other factors (see review by Russell et al. 2001).

Following a decade of sustained low deer densities, some hunting regulations that had allowed effective control over deer populations were changed. Specifically, overall harvest allocations for the wildlife management unit (WMU) encompassing the majority of the KQDC were reduced by as much as 50 percent, DMAP antlerless tags were decreased, and the 2-week concurrent antlered and antlerless season was shortened by a week. Consequently, deer populations within the KQDC increased by 60 percent in the relaxed DMAP era relative to the prior DMAP era. This 5-year average masks the true magnitude of the increases as the deer densities have increased steadily since 2017 and are currently almost as high (9.49 deer per sq. km) as they were before the DMAP era (about 10 deer per sq. km). Concomitantly, our results clearly demonstrate that browsing has intensified on woody regeneration, particularly on the most palatable species. The proportion of plots categorized as experiencing low browsing for red maple, hemlock, and striped maple dropped by 11, 13, and 8 percent, respectively, between the DMAP era and the relaxed DMAP era. Despite increases in deer densities and the subsequent increase in browse pressure, during the relaxed DMAP era, frequencies of the most palatable species have remained constant (hemlock, striped maple) or even increased (red maple). Other studies have found that changes in stem densities often lag behind shifts in deer densities as demographic inertia in tree populations, including recruitment, growth, and mortality, are not immediately impacted by browsing (Bradshaw and Waller 2016, Rooney et al. 2002). However, although both black cherry and American beech were not highly preferred, frequencies for both species changed significantly over time, likely because of forest health issues. American beech abundance in forest understories has increased regionally by as much as 350 percent from increased root suckering as mature trees decline from beech bark disease (Garnas et al. 2011). Black cherry is the dominant hardwood in the Allegheny forest canopy and has suffered declines of up to 76 percent in the past 20 years, putatively from diminished nitrogen deposition and increased fungal virulence (Royo et al. 2021).

CONCLUSIONS

Over its 21-year history, the Kinzua Quality Deer Cooperative project has become a world-class demonstration of how adaptive forest and game management, coupled with extensive outreach and communication, can improve both forestry outcomes and hunting outcomes throughout a 306 sq. km managed landscape of public and private ownerships (Reitz et al. 2004, Royo and Stout 2019, Stout et al. 2013). The coordinated approach, coupled with game management policies, was successful in sustaining effective hunting pressure over the resident herds, a task that proves increasingly difficult as the active hunter population drops (Diefenbach et al. 2022). Results from the project have shaped the Pennsylvania Game Commission decisions on deer management over two decades and informed forest monitoring guidelines for the state forests of the Commonwealth of Pennsylvania. Although our results document increased woody regeneration when deer densities were sustained at lower levels, research in browse legacy forests strongly suggests herd reductions on decadal timescales are necessary to regain diverse understory plant communities (McGarvey et al. 2013, Nuttle et al. 2014, Royo et al. 2010, Tanentzap et al. 2012). Hence, the current trajectory of rising deer populations places the gains made in the KQDC area at risk. In fact, during the era of the Deer Management Assistance Program, use of operational-scale fences to protect regeneration dropped drastically throughout the KQDC region (Stout et al. 2013). However, in Pennsylvania, use of fencing has re-emerged as a viable management option to protect and ensure diverse regeneration (Parker et al.

2020). Encouragingly, recent changes to season and bag limits in Pennsylvania expanded Sunday hunting opportunities and reinstated the statewide 2-week antlered and antlerless season (Pennsylvania Game Commission 2021). Further monitoring will be required to assess whether these policies help curb browsing impacts and what effect, if any, rising deer populations over the past 5 years had on overall plant community diversity.

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