RECOGNITION, RESPONSE, AND RECOVERY: DEER IMPACT RESEARCH IN ALLEGHENY HARDWOOD FORESTS

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Insights for Managers

- **Scientists and land managers from this region were among the very first in North America to document deer overbrowsing impacts in forests and to propose the interdependence between forest and game management.**
- **Deer-forest research in the region helped transform forest regeneration inventories into a flexible and biologically realistic stocked plot approach that considers species' growth, survival, and sensitivity to browsing as well as deer browse pressure.**
- **During the 1980s, a groundbreaking controlled browsing experiment was the first to examine how variation in deer browsing and forest overstory conditions could drastically alter and impoverish vegetation, causing long-lasting impacts that permeated throughout insect and animal communities.**
- **Moreover, it was the first experiment to demonstrate how moderate deer densities (i.e., 10 to 20 deer per square mile) are compatible with plant and avian diversity in these forests.**
- **More recently, research suggests that coordinated and adaptive management that engages policymakers, land managers, and hunters can maintain deer herds at healthy densities (~13 deer per square mile) and benefit plant species populations and plant community richness; however, these results occur on decadal timescales.**
- **Our latest findings provide strong evidence of the linkage between forest management activities and deer browse impact. Specifically, these results suggest that when ~20 percent of the landscape within the typical home range of deer contains forage-rich, early-successional habitat, the negative impacts of browsing on vegetation at local (i.e., stand) scales lessen and ultimately disappear.**
- **Taken together, this research provides compelling evidence of the critical role humans play in sustaining diverse forests and healthy herds through management, policy, and recreation decisions. Sustaining and improving the ecosystem services provided by our forests will require continued relevant science and cooperation among policymakers, land managers, and hunters.**

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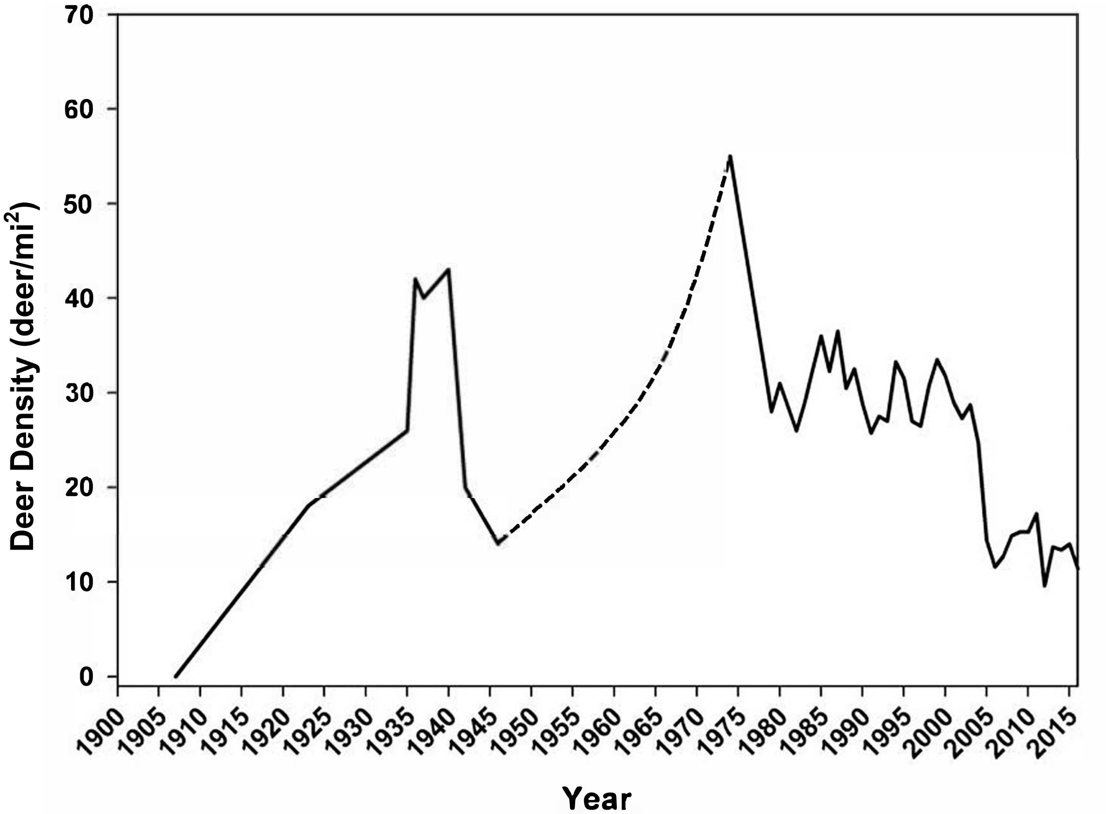

Figure 1.—White-tailed deer population trends in northwestern Pennsylvania, 1907-2017. Dashed curve represents a time period (1947-73) for which no quantitative data are available, but for which we assume an exponential increase in populations as timber harvesting increased in the late 1950s and 1960s. The sharp decline observed beginning in 2003 is a direct result of the targeted deer harvests within the KQDC project area.

INTRODUCTION

During the early decades of the 20th century the confluence of two major alterations to forest and wildlife population dynamics occurred in the northern tier of Pennsylvania; namely, the near-complete harvesting and resultant regrowth of all forests in the region coupled with the extirpation and subsequent reintroduction of white-tailed deer (*Odocoileus virginianus*) (Redding 1995). In the ensuing years, abundant early-successional habitat, the absence of apex predators such as wolves and mountain lions, and lax game management policies resulted in a population explosion of deer to levels that far exceeded precolonial estimates (<11 deer per square mile) (McCabe and McCabe 1997) and that were generally above levels compatible with healthy forest regeneration (≤20 deer per square mile) (Horsley et al. 2003; Fig. 1).

By the early 1930s deer populations exceeded carrying capacity throughout the forests of northern Pennsylvania and were causing damage to tree regeneration and understory plant communities. This was documented in some of the earliest papers about deer browsing impacts in the scientific literature (Ehrhart 1936, Frontz 1930, Ostrom 1937). For example, Ashbel Hough, an early USDA Forest Service Northeastern Research Station scientist working in the Allegheny National Forest, declared it was evident that deer overbrowsing had nearly eradicated understory hemlock (*Tsuga canadensis* L.) and witch hobble (*Viburnum lantanoides* Michx.) throughout the Tionesta Old Growth forest during the 1930s (Hough 1965). Several other researchers and managers sounded similar alarms (Gerstell 1938, Leopold et al. 1947, McCain 1941). This initial period of deer overabundance, however, lasted only a couple decades. Toward the end of the 1930s, deer herds faced an ever-diminishing carrying capacity as forests grew into forage-poor stem-exclusion (sapling) conditions which, coupled with successive severe winters beginning in 1938-39, caused deer populations to collapse to approximately 14 per square mile by 1946 (Hough 1949). Given the collapses in deer numbers and reductions in the local timber industry with the onset of World War II and because of the widespread stocking of nonmerchantable sizes classes, deer population data were not gathered between 1947 and 1973. However, as the maturing second-growth forests began to yield sawlog-size timber and forest industry returned, deer populations climbed. By 1960, even-aged silvicultural systems were once again utilized by a burgeoning forest industry and, with the concomitant creation of forage-rich, early-successional habitat, deer populations rebounded and remained excessively high throughout much of latter half of the 20th century (Jordan 1967, Redding 1995).

By the late 1960s regeneration failures following even-aged harvests were commonplace. The USDA Forest Service Research branch responded to the requests of local land managers for help in solving these issues and initiated a coordinated research agenda to assess the causes of these failures and to provide guidelines for managers to sustainably regenerate forests. From very early on, researchers strongly suspected deer contributed to the regeneration failures (Grisez 1959, Jordan 1967, Shafer et al. 1961). Over the following five decades the Northeastern Forest Experiment Station, now known as the Northern Research Station (NRS), conducted a series of related experiments to elucidate the role white-tailed deer played in shaping forest dynamics and biodiversity. Over time this research program evolved. After seminal exclosure studies documented browse impacts on regeneration, complex manipulative studies assessed browse legacies on biodiversity across a range of deer densities and forest conditions. These were followed by long-term monitoring of vegetation changes across landscapes after deer herds were reduced. The current, culminating experiment is testing how variation in habitat composition at large spatial scales affects browse impact at local scales. Collectively, this body of work is internationally recognized as very important, provides solutions to important management problems, and informs policy.

THE GROWTH AND DEVELOPMENT OF A RESEARCH PROGRAM

Recognition of Deer Impact on Regeneration

In 1967 researchers in the Northeastern Forest Experiment Station initiated a study to ascertain how frequently and under which conditions regeneration failures occurred. Although the research did not explicitly consider deer, researchers knew that browsing reduced advance regeneration abundance and, therefore, could be directly responsible for the regeneration failures. Using preharvest and postharvest regeneration tallies in 65 operational even-aged regeneration harvests on the Allegheny National Forest, researchers revealed that 46 percent of the harvests failed to successfully regenerate forests following clearcuts (Grisez and Peace 1973). Moreover, researchers found that the single best predictor of which areas would regenerate successfully was whether stands contained abundant and well-distributed advance regeneration. These and other results (e.g., Leak 1969) on the importance of both abundance and spatial distribution of regeneration in predicting regeneration success led to a shift in inventory methods. Many foresters did not conduct understory inventories before harvests, and when this was done, decisions were based on the number of advance seedlings per acre. The NRS developed a "stocked plot" concept wherein decisions were made based on the proportion of plots that met acceptable stocking criteria (Grisez and Peace 1973, Marquis et al. 1975).

In tandem with the regeneration outcomes study, scientists capitalized on a set of deer-excluding fences and paired areas subject to ambient browsing in 13 clearcuts throughout the Allegheny National Forest. These clearcuts were established in the 1950s and 1960s to determine the degree to which white-tailed deer were responsible for regeneration failures. Marquis (1974) and colleagues found that of the 13 stands, 12 (92 percent) successfully regenerated within the fence, whereas only 5 (38 percent) regenerated under ambient browsing. Moreover, when analyses were restricted to the 8 stands that failed to regenerate under ambient browsing, in 7 of the 8 cases exclosures resulted in successful regeneration. Hence, Marquis (1981) concluded deer were directly responsible for 87 percent of the regeneration failures in clearcuts in the Allegheny Plateau region. Researchers also noted that the conditions required for regeneration success differed between treatment areas. Within fences regeneration success was achieved with far fewer seedlings. This recognition established the foundations for more flexible and biologically realistic stocking criteria that varied in response to deer browse pressure. Early guidelines focused on black cherry (*Prunus serotina* Ehrh.), the most abundant species at the time, whereas, over time, guidelines were developed to include other species with different growth and survival rates as well as variation in sensitivity to deer browsing (Brose et al. 2008, Marquis and Bjorkbom 1982, Marquis et al. 1992).

Forest Diversity Responses to Variable Deer Densities

Following the experimental confirmation that overbrowsing was largely responsible for regeneration failures and the associated work on developing silvicultural guidelines given deer browsing, (e.g., fencing, fertilizer) (Marquis and Brenneman 1981), the question then became understanding how different deer densities would affect forest diversity. To address this, the Northeastern Forest Experiment Station initiated a groundbreaking controlled browsing experiment. In this study, vegetation responses in uncut, thinned, and clearcut areas were monitored for 10 years under 4 different deer densities: 10, 20, 38, and 64 deer per square mile (Horsley et al. 2003, Tilghman 1989). This seminal work conclusively demonstrated that the rate and trajectory of regenerating forest communities are strongly mediated by deer browsing and vary with the sensitivity of species to deer browsing.
Specifically:

- More palatable or browse-intolerant species such as brambles (*Rubus* L. spp.), red maple (*Acer rubrum* L.), and birch (*Betula* L. spp.) decreased in abundance and were limited in height.
- Increasing deer densities favored species such as black cherry and hay-scented fern (*Dennstaedtia punctilobula* Michx. Moore) that are tolerant to browsing or are avoided by deer (Horsley et al. 2003, Nuttle et al. 2014, Tilghman 1989).
- Selective browsing impacts to species were so pronounced that species composition and diversity changed depending on the level of browse pressure. At higher deer densities, regenerating forest stands became depauperate and strongly dominated by browse-tolerant species; at the lowest deer densities the fast-growing and highly palatable pin cherry (*Prunus pensylvanica* L.f.) flourished and suppressed regeneration of other hardwood species (Ristau and Horsley 1999, 2006).

These findings suggest that the relationship between deer browsing and forest regeneration may be unimodal: high deer herbivory pressure facilitates dominance by browse-tolerant species, and light herbivory pressure promotes dominance by fast-growing pioneer species. Thus, forest productivity and diversity may be highest under moderate browse pressure (see also Royo et al. 2010a). Indeed, the authors suggested that densities of 20 deer per square mile would be compatible with hardwood regeneration, although somewhat lower densities (~10 deer per square mile) may be necessary to restore diversity to the overall plant community.

This landmark study also revealed that by altering the patterns of vegetation development and composition, deer browsing can alter the diversity and dynamics across trophic levels. For example, deCalesta (1994) found that the suppression of tree regeneration into the midstory by deer browsing reduced intermediate canopy nesting bird richness and abundance by 30 percent and 37 percent, respectively (see also McGuinness and deCalesta 1996). As these stands matured, these direct and indirect deer-induced changes to forest vegetation composition and structure "ricocheted" throughout the trophic chain (deer → tree → insect → bird communities) causing declines in insect and bird densities 30 years after stand establishment (Nuttle et al. 2011). Deer-induced changes to vegetation dynamics and composition altered other interspecific interactions. For example, the dense and persistent hay-scented fern layer promoted by excessive browsing (Nuttle et al. 2014) exerts a strong competitive effect on tree seedlings and secondarily enhances seed and seedling predation rates by small mammals, thus further suppressing tree establishment (Horsley 1993, Royo and Carson 2008).

Monitoring Recovery and Impact across Landscapes

By the beginning of the 21st century, browsing-induced changes to forests were so extensive that the very baseline of what constitutes a normal forest had shifted (Stout and Horsley 2004). Forest managers often had to employ extraordinary measures including herbicide applications to control interfering vegetation, fencing to mitigate deer browsing, or both, to sustain diverse and abundant seedling recruitment on a stand-by-stand basis (Marquis et al. 1992). Moreover, researchers acknowledged that the degraded habitat conditions throughout the landscape would continue to complicate management and be unfavorable to the deer herd and, by extension, to the hunting experience. Thus, beginning in 2000, a group of private and public land managers, scientists, hunters, and others began working across a 74,350-acre landscape on an adaptively managed and cooperative project whose joint goal was to improve forest habitat, deer herd health, and the hunting experience. The group used newly available deer management programs offered by the Pennsylvania Game Commission, most importantly the allocation of additional and targeted antlerless hunting permits, to begin the ambitious Kinzua Quality Deer Cooperative (KQDC) management and monitoring project (Reitz et al. 2004, Stout et al. 2013).

Within the KQDC, aggressive deer harvests coupled with strong hunter engagement resulted in a rapid and sustained reduction in deer densities of approximately 50 percent (Figure 1). Vegetation monitoring results demonstrated that browsing on hardwood species inversely tracked deer densities: as deer densities decreased, browsing also decreased. By 2007, 3 years after deer herd reductions, populations of known browse-sensitive phytoindicators including *Trillium* L. spp., *Maianthemum canadense* (Desf.) and *Medeola virginiana* (L.) experienced substantial (32 percent to more than 100 percent) increases in abundance, size, and reproductive success (Royo et al. 2010b). Similarly, regeneration of browse-sensitive tree species including red maple (316 percent increase), sugar maple (*A. saccharum*; 382 percent increase), birch (438 percent increase), white ash (*Fraxinus americana* L.; 466 percent increase) improved in the 12 years following herd reductions. Additionally, cucumber magnolia (*Magnolia acuminata* L.), a browse-sensitive species virtually absent at the start of the monitoring, became the 5th most common species in the regeneration layer by 2016. As tree recruitment improved across the landscape, fencing of regeneration harvests, a management recommendation triggered when desirable regeneration is scant or at risk

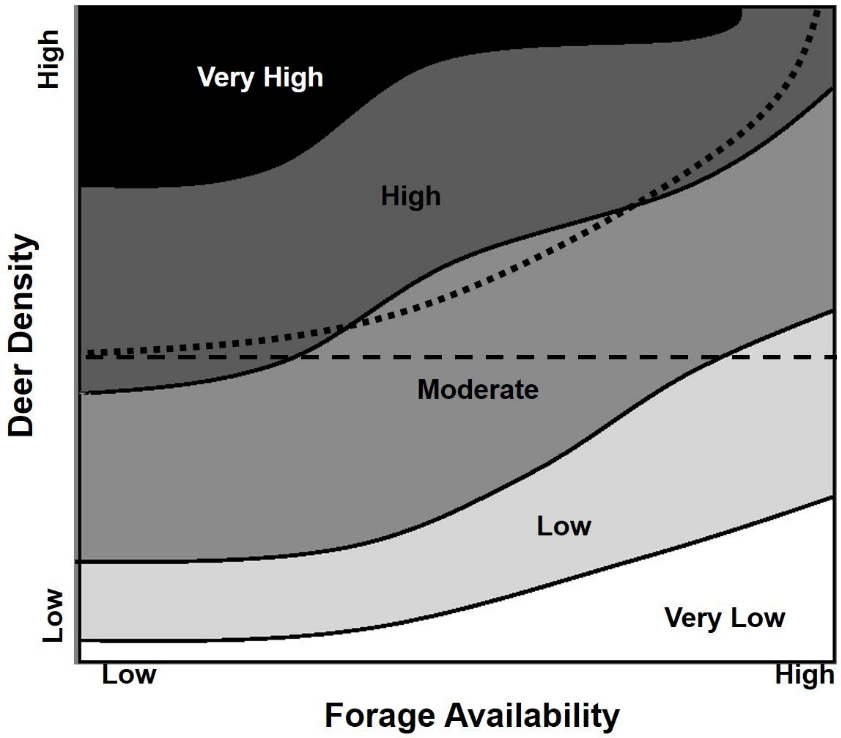

Figure 2.—Conceptual model illustrating local browse impact (shaded isoclines) as a function of deer density and forage availability. Dashed line illustrates a constant ungulate density exerting high to low impact depending on forage availability. Dotted line represents an ungulate population that increases over time as forage increases, thus nullifying any forage-mediated reductions in browse impact.

of herbivory, plummeted. Indeed, Collins-Kane Hardwood, one of the participating land managers of the KQDC, experienced a decline in fenced acreage from an average 129 acres/year to zero (with associated savings that averaged of $22,712/year) while other landowners like the Allegheny National Forest stopped erecting fences within the KQDC entirely (Stout et al. 2013). Lastly, after more than a decade of sustained deer herd reductions, the baseline itself shows signs of shifting again to conditions representative of what our forests might look like without too many deer. In addition to the responses detailed above, vascular plant species richness within the KQDC increased by 12.6 percent at the small plot level (number of species/m^2) and by 16.2 percent whole plot (0.3 acre) scale by 2016, 14 growing seasons after lowering the deer herds (Royo, unpubl. data[2]). Continued monitoring will ascertain whether these increases in species richness persist. But what is clear is that recovery of the plant community requires a sustained commitment to maintaining deer herds at a level compatible with their habitat on decadal timescales.

In the first decade of the KQDC project, private land partners created about 11,000 acres of early successional habitat through timber harvests (~15 percent of the land area enrolled in the KQDC) as the Allegheny National Forest conducted the environmental analyses necessary to concentrate harvesting throughout its landholdings enrolled in the KQDC during the second decade. Interestingly, private land managers achieved diverse regeneration of their harvests without fencing, even though their properties often had higher deer densities than the National Forest lands. These observations bolstered a hypothesis that was formulated based on evidence from the controlled browsing experiment that deer impact on forest vegetation is a joint function of deer density and the amount of forage available to deer within their home range (Fig. 2) (Marquis et al. 1992). This hypothesis extends the concept of the ecological carrying capacity by considering the habitat's influence on the deer herd and the reciprocal impact of the deer herd on the habitat (deCalesta and Stout 1997).

[2] Royo, A.A. 2016. Kinzua Quality Deer Cooperative summer 2016 data. On file at USDA Forest Service, NRS-02, Irvine, PA 16365.

From a forest management perspective, the concept that variability in habitats at large scales could modulate browse impacts locally was attractive because it suggested a solution whereby land managers could proactively counter overbrowsing by creating forage-rich, early-successional habitat at the appropriate spatial and temporal scales (deCalesta and Stout 1997, Miller et al. 2009). Despite the appeal, empirical support of this concept remained generally anecdotal. For example, during the 1980s, high browse impact and regeneration failures were prevalent throughout the Allegheny National Forest, where harvest rates at the time created relatively low proportions of forage-producing habitat (4 percent clearcut + 13 percent thinned). In contrast, even under high deer densities, regeneration failures did not occur where forage-producing habitat was abundant either in the controlled browsing study (10 percent clearcut + 60 percent thinned) (Horsley et al. 2003) or in a nearby 1100-acre demonstration area (13 percent clearcut + 33 percent thinned) (Stout et al. 1995).

To rigorously test the hypothesis that deer impact on vegetation was a function of both deer density and forage availability, the NRS initiated a deer impact study in 2012: a large-scale hybrid experimental approach that incorporates a manipulative (fence/control) treatment to test how localized (stand-level) browse impact by white-tailed deer varies among 23 broadly distributed sites that vary in deer densities and relative abundance of various habitat types at larger (640-acre) scales. The area characterized was specifically chosen to encompass the typical home-range size of deer within northern hardwood forests (Tierson et al. 1985). This study emphasized the proportion of forage-rich habitats created by management (recent [≤5 years] timber harvests + herbaceous openings [including oil and gas openings and pipelines] + agricultural areas) versus forage-poor habitats (stem-exclusion stands; clearcut areas >5 years, but ≤17 years). Initial results from this study suggest that while deer browsing reduced plant community richness and cover by as much as 53 and 70 percent, respectively, browse impact varied in response to the relative abundance of forage containing habitats. Specifically, relative to fenced areas, browse impact weakened and ultimately disappeared as the proportion of forage-rich habitats created by management increased to ≥20 percent. Conversely, vegetation grew increasingly depauperate as landscapes contained greater proportions of forage-poor habitats, particularly when browsed (Royo et al. 2017).

These preliminary results demonstrate that even-aged forest management, when practiced at the appropriate scales, can alleviate browse pressure in the near term. The results also strongly suggest that the effect is temporally dynamic, because changes to vegetation structure, composition, and abundance that occur during succession eventually reverse and intensify browse impact. Stated plainly, harvest operations create forage-rich habitats that initially mitigate browsing; however, as these areas mature into forage-poor, stem-exclusion habitat, deer browsing intensifies on any remaining areas that still provide forage. As this experiment matures and yields further data, we hope to refine our guidelines on the spatial and temporal scales of forest management operations that simultaneously provide complementary benefits to wildlife, biodiversity, and sustainable management. Moreover, these data will allow us to refine recently developed forest dynamics models that explicitly consider how forage quantity and quality at various scales can modulate browse pressure on regenerating forest stands (LANDIS-II) (De Jager et al. 2017).

SUMMARY

Since the early 1900s, forest and game management practices across the northern tier of Pennsylvania have created an exceptional model system in which to study deer-forest interactions. Fortuitously, Forest Service researchers and a cadre of engaged public and private land managers have unswervingly studied these dynamics for nearly a century. The international scientific community recognizes this body of work, which provide guidelines for key management issues regionally. This long-term research program is a model of the steady and accumulative progress that is fundamental to discovery. Early ideas or hypotheses were tested by experimentation and the results, over time, were distilled into a more accurate understanding of the system. For example, as early as 1936, Ira Gabrielson commented on the interdependence of forest habitat and deer and reasoned that concentrating harvests within a landscape up to a threshold amount of 25 percent may benefit plants and wildlife (Gabrielson 1936). Nearly 85 years later, landscape-level studies such as the KQDC and deer impact studies are finally providing empirical evidence to refine these ideas and provide meaningful guidelines.

The research trajectory on the linkage between forest health and deer also compels us to recognize the critical role humans play in sustaining diverse forests and healthy herds through management, policy, and recreation decisions. Policies can help maintain populations within healthy limits, particularly given the decline in numbers of hunters (Diefenbach et al. 2005). By the same token, land managers can sustainably create young forest habitat (early successional) to improve deer conditions and engage hunters who help regulate herd density. Only by engaging all three key stakeholders—policymakers, land managers, and hunters—can we sustain and improve on various ecological services provided by forest communities over the next century.

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