

Plant Communities Growing on Boulders in the Allegheny National Forest: Evidence for Boulders as Refugia from Deer and as a Bioassay of Overbrowsing

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ABSTRACT: Deer have been overabundant throughout much of Pennsylvania since at least the 1940's. We compared plant communities in the Allegheny National Forest (ANF) on boulder tops and the forest floor to test the hypothesis that large boulders serve as refugia for plants threatened by deer herbivory. Five of the ten most common woody species (hemlock, *Tsuga canadensis* L., mountain maple, *Acer spicatum* Lam., red maple, *A. rubrum* L., striped maple, *A. pensylvanicum* L., and yellow birch, *Betula alleghaniensis* Britton) occurred at much higher densities on boulders than in randomly selected areas of the same size adjacent to these boulders on the soil surface. We never encountered any individuals of hemlock, mountain maple, or red maple on the forest floor. Total woody species density (excluding root suckers of beech, *Fagus grandifolia* Ehrh.) was nearly three times higher on the boulders. Woody species richness and evenness, as well as forb and shrub cover and richness, were also much greater on boulders. Our results strongly suggest that overbrowsing by deer can dramatically reduce tree regeneration and diversity as well as reduce forb and shrub abundance in the ANF. Furthermore, understory plant communities are now dominated by species that are known to be unpalatable or tolerant of deer browse, particularly beech, grasses, and ferns (*Dryopteris carthusiana* Vill. and *Thelypteris noveboracensis* L.). The primary alternative explanation is that conditions on the surface of boulders are superior for numerous woody and herbaceous species. Although we cannot rule this out, we consider this alternative improbable because of the poor nature of these habitats.

Because deer are reducing the diversity and abundance of both woody and herbaceous species, we conclude that deer are damaging the very nature of these hardwood forests. Furthermore, our findings suggest that boulders could serve as an inexpensive bioassay of deer impact on vegetation whenever they are common and large enough. Boulders may also overcome the problem associated with the ghost of herbivory past, whereby plant species that would respond to the reduction of herbivores are absent because they have been driven to very low abundance or local extirpation. Our findings suggest that sampling the surface of boulders circumvents this problem because the vulnerable species were never subjected to sustained browsing on these refugia; consequently, these areas may represent typical levels of abundance of these vulnerable plant species.

Index terms: beech, browsing, ferns, forest regeneration, herbivory, herbs, refugia, species richness, white-tailed deer

INTRODUCTION

There is growing evidence that browsing by high populations of white-tailed deer (*Odocoileus virginianus*) can dramatically reduce the diversity, abundance, and vigor of both woody and herbaceous species in eastern deciduous forests (Miller et al. 1992, Balgooyen and Waller 1995, Waller and Alverson 1997, Augustine and Frelich 1998, Webster et al. 2001, Collins and Carson 2003, Horsley et al. 2003, and a review by Russell et al. 2001). In the Allegheny National Forest (ANF), overabundant deer substantially reduce the regeneration of hardwoods and hemlock, cause declines in herbaceous species, and lead to an increase in the abundance of unpalatable fern species (Hough 1965, Marquis 1975, Bjorkbom and Larson 1977, Horsley and Marquis 1983, Whitney 1984, Tilghman 1989, Whitney 1990, Horsley 1993, Rooney and Dress 1997).

Heavy deer browsing can restrict vulner-

able and palatable species to deer refugia though only a small number of these refugia have been documented. For example, following a tornado blowdown in the Allegheny National Forest (ANF), Long et al. (1998) found that hemlock saplings and seedlings were larger and more abundant on tree tip-up mounds compared to areas on the forest floor. They showed that large tip-up mounds were less accessible to deer, and thus were one of the few sites with abundant hemlock regeneration. They acknowledged that tip-up mounds might enhance the growth and density of hemlocks; however, this appeared unlikely because mounds experience dramatic erosion, freezing, and desiccation; conditions typically inimical to hemlock germination and survival (Long 1998; see also Schopmeyer 1974, Beatty 1984, Godman and Lancaster 1990, Peterson et al. 1990). Grisez (1960) showed that browsing damage was lower and overall woody seedling density (subtracting beech) higher within piles of hardwood slash (leftover from

clear-cutting) when compared to areas that are more open. Apparently, the slash protected the seedlings from browsing, and this protection increased with the height of the pile of slash. Additionally, Rooney (1997) found that large boulders in the ANF had abundant and vigorous populations of the highly palatable Canada mayflower (*Maianthemum canadense* Desf.), whereas small boulders that were easily reached by deer had sparse populations. An herbaceous species (wood-sorrel, *Oxalis acetosella* L.) that was unpalatable to deer did not differ in abundance between small and large boulders.

The abundance of a vulnerable herb on top of large boulders (Rooney 1997) suggests two intriguing possibilities. First, that boulders and rock outcrops may serve as important refugia for a whole suite of plant species that are vulnerable to browsing. Such refugia could serve as a storehouse of genetic diversity for these vulnerable species and as the origin for their subsequent spread if deer browsing is brought under control. Second, these sites could serve as an inexpensive bioassay of deer impact on forest health and biodiversity. Currently, one of the primary methods to gauge the impact of deer on forests is to construct fenced exclosures. These exclosures are expensive to build and maintain. Additionally, they require a long-term commitment by researchers to verify the extent of overbrowsing, because it may take years for vulnerable species to recolonize the protected areas if these species have been locally extirpated or have poor dispersal or both. We term this lag-time the ghost of herbivory past (sometimes called a legacy effect) and suggest that boulders may be a rapid and inexpensive method to assay the impact of too many deer. We recognize that this approach has obvious difficulties (see discussion), but nonetheless, we feel it has potential. One of our goals was to gauge this potential.

We tested the hypothesis that large boulders in the ANF serve as refugia from deer, and thus we predicted that boulders would have a higher abundance and diversity of both woody and herbaceous species. Furthermore, we predicted that the species growing on boulders would be those that

are considered vulnerable or sensitive to deer browsing.

METHODS

The ANF is located in northwestern Pennsylvania and covers over 207,195 contiguous hectares. Predominant tree species are black cherry (*Prunus serotina* Ehrh.), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh), oak (*Quercus* spp.), birch (*Betula* spp.), beech (*Fagus grandifolia* Ehrh.), and eastern hemlock (*Tsuga canadensis* L.) (Sundquist et al. 1990). Taxonomy follows Gleason and Cronquist (1991). The climate is cool and humid, with 106.7 cm of precipitation per year and an average annual temperature of 7.8 °C. Elevations in the ANF range from 457–597 m above sea level. The soils are strongly acidic (pH 5.1–5.5) stony or sandy loams, consisting of sandstone, conglomerate, and shales (Bjorkbom and Larson 1977).

We sampled plant species in July 1999 and June 2000 along Forest Route 133 (FR 133), which is directly to the east of the ANF Tionesta Scenic Reserve, an old-growth beech-hemlock forest (see Bjorkbom and Larson 1977). The boulders are actually large sections of cross-bedded sandstone that broke off from the substrate and slid down the steep hillsides in the distant past. We avoided strongly sloping boulders, and selected boulders that were flat enough to accrue a layer of organic matter that would allow for vegetation establishment. Boulders were at least 1.5 m off the ground at their lowest point although most were higher. Although we recognize that deer can jump higher than 1.5 m, this height apparently precluded deer access because we never found any evidence of deer browse, scat, or hoof prints on the boulders sampled. Conversely, signs of deer were ubiquitous on the forest floor at every location. In 1999, we delineated the area of the surface of each boulder, and identified and counted all saplings ≥ 30 cm in height and < 5 cm in diameter at breast height. We then randomly selected an adjacent site of the same surface area approximately 3 m away from the boulder on the forest floor and censused all saplings

in the same manner. In 2000, we assessed herbaceous species richness and visually estimated percent cover of each species in three randomly placed, 1 m² plots on the surface of each boulder and on the adjacent forest floor. Finally, we censused all plant species on surface of the boulders and adjacent control plots to quantify total species richness.

We used paired t-tests to compare the density, species richness, and species evenness (Shannon-Wiener Index, Magurran 1988) of saplings to determine if woody species were larger and more abundant on boulders than on the forest floor. Similarly, we used paired t-tests to test the hypothesis that herbaceous diversity and abundance are greater on boulders. Species overlap between treatments was examined using Sorensen's index (Magurran 1988) calculated using percent cover data. This index ranges from 0 to 1, and the higher the value the more similar the vegetation between the two locations.

RESULTS

We surveyed 12 boulders ranging in surface area from 13.6 m² to 70.5 m² with an average surface area of 37.1 m² (± 1 SE 4.5 m²) in 1999, and 7 boulders ranging in surface area from 7.6 m² to 125.0 m² within average surface area of 56.8 m² (± 1 SE 9.9 m²) in 2000.

Tree species

The densities of hemlock (*Tsuga canadensis* L.), mountain maple (*Acer spicatum* Lam.), red maple (*Acer rubrum* L.), striped maple (*Acer pensylvanicum* L.), and yellow birch (*Betula alleghaniensis* Britton) were significantly higher on the surface of the boulders than on the forest floor (Figure 1). Of the 10 species we encountered, only beech, a species that commonly root sprouts, was significantly more abundant on the forest floor. Total woody species stem density was not significantly different; however, when beech was excluded from the analysis, density on the surface of the boulders was nearly three times the density on the forest floor (Figure 1). Although beech was dominant off the boulders, we

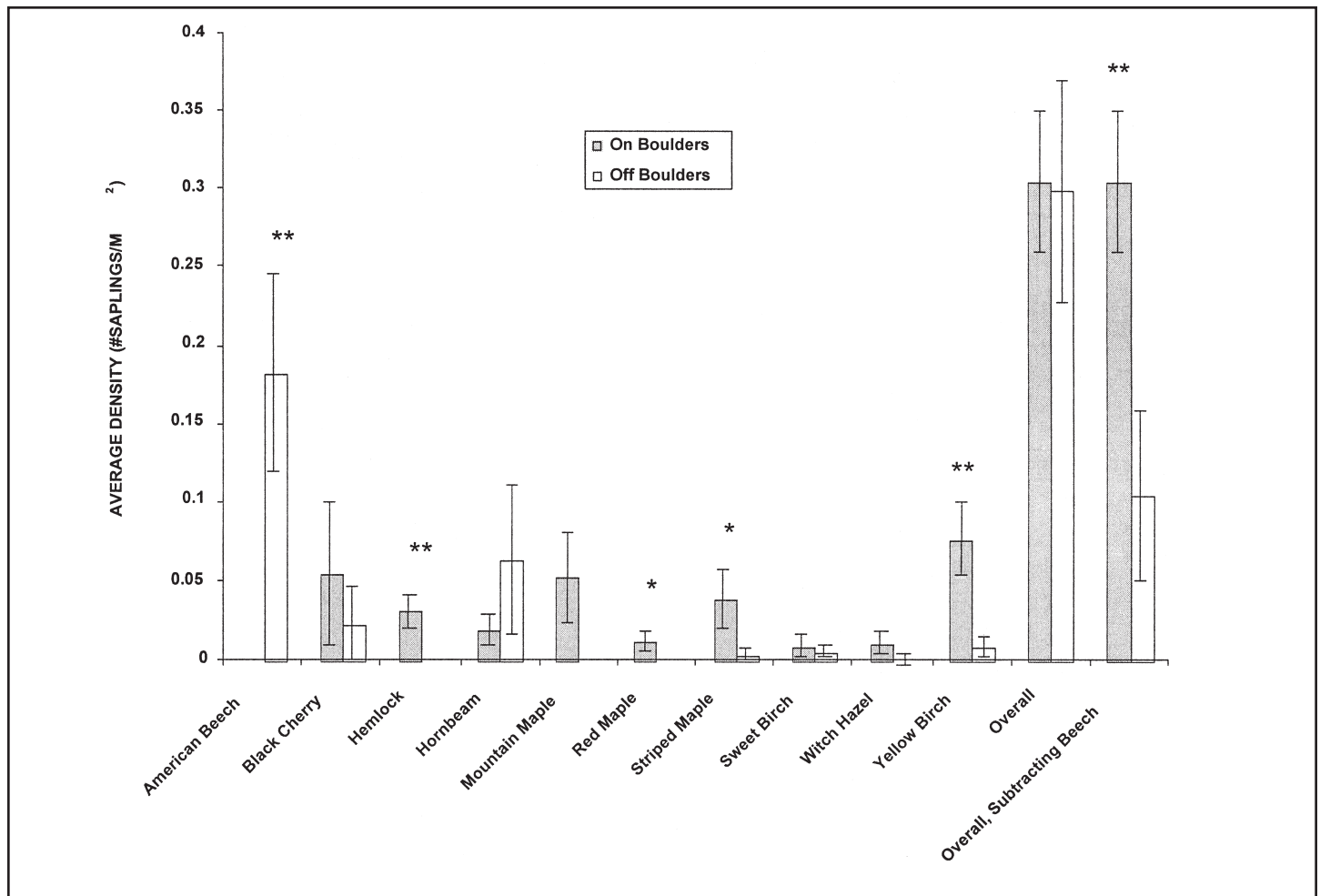


Figure 1. Mean sapling densities on the surface of boulders and on the forest floor. The bars represent ± 1 standard error. The P-values are from paired t-tests (* = <0.05 , ** = <0.01). There was no hemlock, mountain maple, or red maple found on the forest floor and no beech found on the surface of boulders.

did not detect a significant negative relationship between the density of beech and the density of other tree species growing on the forest floor ($R^2 = 0.1393$, $P = 0.8$). Both mean species richness and mean evenness were significantly greater on boulders than on the forest floor (species richness = 3.3 and 1.8, $P < 0.02$; evenness $H = 2.0438$ and $H = 1.0947$, $P < 0.0001$; respectively).

Herbs and shrubs

The cover of *Mitchella repens* L., *Rubus* spp., and *Polypodium virginianum* L. were significantly higher on the surface of the boulders versus the forest floor.

The mean total percent cover for all understory taxa, all forbs combined, and all

shrubs combined was also significantly higher on the surface of boulders (Table 1, Figure 2). Overall, mean species richness did not differ between the two locations (boulder = 9.1 and forest floor = 8.6; $P < 0.34$). Composition did differ, however, between the two sites. Ferns and grasses predominated on the forest floor (74.7% relative cover) whereas forbs and shrubs predominated on the surface of boulders (70.2% relative cover). Consequently, the similarity between these adjacent sites was quite low (Sorensen's Measure 0.163). The only abundant fern on the boulders was rock fern (*Polypodium virginianum* L.), the preferred habitat of this species. The richness of the forb and shrub community was significantly higher on the surface of boulders (boulder = 5.9, forest floor = 4.3, $P < 0.06$). We never observed a shrub species growing on the forest floor.

DISCUSSION

Do boulders serve as refugia for plant species?

Our goal was to test the hypothesis that the surface of large boulders would serve as a refuge from overbrowsing by deer, and thus these sites would have a higher density and diversity of both herbaceous and woody species. Our results were entirely consistent with this hypothesis. We found that hemlock, mountain maple, red maple, striped maple and yellow birch were much more abundant on boulders, and overall tree species diversity was greater on these boulders. The abundance and regeneration of all of these species can be severely reduced by deer browsing (Stoeckeler et

Table 1. The mean percent cover of herbaceous species and shrubs on boulders and on the forest floor. Dash lines (-) indicate species was not present. Asterisks (*) indicate species was present but found outside the 1m² sample plots used to estimate cover.

Species	N	Boulder Top	Forest Floor
Graminoids			
<i>Agrostis</i> spp.	2	0.29	2.54
<i>Brachyelytrum erectum</i> Schreb.	2	-	1.7
<i>Carex pensylvanica</i> Lam.	1	-	0.21
<i>Carex</i> spp.	1	*	0.21
<i>Panicum</i> spp.	1	-	0.21
Graminoids Total		0.29	4.87
Ferns & Clubmosses			
<i>Dennstaedtia punctilobula</i> (Michx.)			
Moore	2	-	6.8
<i>Dryopteris carthusiana</i> Vill.	5	3.58	28.1
<i>Dryopteris intermedia</i> Muhl.	4	8.2	*
<i>Lycopodium complanatum</i> L.	2	1.2	7.6
<i>Lycopodium obscurum</i> L.	4	*	3.1
<i>Onoclea sensibilis</i> L.	1	-	4.1
<i>Polypodium virginianum</i> L.	5	16.3	-
<i>Thelypteris noveboracensis</i> (L.) Nieuwl.	4	-	20.1
Ferns & Clubmosses Total		29.28	69.8
Forbs			
<i>Aralia nudicaulis</i> L.	1	6.1	-
<i>Arisaema triphyllum</i> (L.) Schott	2	0.7	0.21
<i>Clintonia borealis</i> (Aiton) Raf.	2	5.6	-
<i>Coptis trifolia</i> (L.) Salisb.	2	0.001	1.5
<i>Cypripedium acaule</i> Aiton	1	-	*
<i>Maianthemum canadense</i> Desf.	7	5.7	12.4
<i>Medeola virginiana</i> L.	2	1.7	1.7
<i>Mitchella repens</i> L.	5	27.23	2.3
<i>Oxalis acetocella</i> L.	4	5.4	4.1
<i>Polygonum cilinode</i> Michx.	2	*	-
<i>Trientalis borealis</i> Raf.	1	-	*
<i>Trillium grandiflorum</i> (Michx.) Salisb.	1	-	0.85
<i>Trillium</i> spp.	1	-	0.21
<i>Trillium undulatum</i> Willd.	1	*	-
Unknown	1	0.001	-
<i>Viola macloskeyi</i> F. Lloyd	2	3.5	-
<i>Viola</i> spp.	3	-	0.85
Forbs Total		55.932	24.12

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al. 1957, Beals et al. 1960, Hough 1965, Stiteler and Shaw 1967, Nixon et al. 1970, Sotala and Kirkpatrick 1972, McCaffery et al. 1974, Skinner and Telfer 1974, Marquis 1975, Bauer 1977, Alverson et al. 1998, McCullough 1985, Anderson and Loucks 1979, Tilghman 1989, Balgooyen and Waller 1995, Johnson et al. 1995, Long et al. 1998, Horsley et al. 2003). Even striped maple, a species considered browse tolerant or unpalatable, was significantly more abundant on the surface of boulders (e.g., Tilghman 1989). This suggests that heavy browsing can reduce the abundance of even this species (see e.g., Webb et al. 1956, Stiteler and Shaw 1967).

Beech was the only woody species that was significantly more abundant on the forest floor than on boulders. Deer do not prefer this species even though they will browse beech in winter if other woody browse is unavailable (Webb et al. 1956, Stiteler and Shaw 1967, Bjorkbom and Larson 1977, Blair and Brunett 1980). Beech can withstand heavy browsing because, unlike the other woody species, many of the saplings are root sprouts (clonal) and thus have a reliable carbon source supplied by large parent trees (Jones and Raynal 1986). Whitney (1984) found that the bulk of beech saplings in the Heart's Content area of the ANF were root sprouts and that this species rarely recruited from seed. A haphazard survey of beech near our site confirmed that the vast majority of the beech saplings were root sprouts (Carson pers. observation). Thus, beech trees were likely absent on the surface of boulders because their seeds were not successful and their root sprouts could not penetrate through rock. Conversely, beech was abundant on the forest floor because it is not preferred and, even when browsed, is tolerant because of its clonal nature.

Herbs and shrubs

A forb and shrub community predominated on the surface of boulders and a grass and fern community predominated on the forest floor (Figure 2, Table 1). Indeed, no shrubs were found on the forest floor! Numerous studies have demonstrated that overbrowsing can depress the performance,

Table 1. Continued from preceding page.

Species	N	Boulder Top	Forest Floor
<i>continued from preceding page</i>			
Shrubs			
<i>Amelanchier</i> spp.	1	*	-
<i>Lonicera canadensis</i> Marshall	3	*	-
<i>Ribes</i> spp.	1	1.6	-
<i>Rubus allegheniensis</i> Porter	6	12.68	-
<i>Rubus occidentalis</i> L.	1	*	-
Shrubs Total		14.28	0
# of Species		24	23

abundance, and diversity of many of the species that were abundant on the boulders, as well as other shrubs and wildflowers (Miller et al. 1992, Balgooyen and Waller 1995, Waller and Alverson 1997, Augustine and Frelich 1998, Webster and Parker 2000, Fletcher et al. 2001, Webster et al. 2001). Species known to be unpalatable, or tolerant to browsing (or both), had high relative abundance on the forest floor (Lay 1969, Korschgen et al. 1980, Sauer et al. 1969, Stromer and Bauer 1980). A number of these species have increased dramatically in eastern deciduous forests throughout the last century almost certainly because of heavy browsing (Horsley and Marquis 1983, Horsley 1993, Tilghman 1989, Rooney and Dress 1997, de la Cretaz and Kelty 1999, Hill and Silander 2001).

There are alternative explanations for our results, but we consider these unlikely and not parsimonious though we cannot rule them out. First, boulders might be better early germination and establishment sites than the forest floor though this seems improbable because many woody and herbaceous species grow best in moist, well-drained soils (Schopmeyer 1974, Bratton 1976, Beatty 1984, Antos 1988, Erdmann 1990, Gabriel and Walters 1990, Godman and Lancaster 1990, Lamson 1990, Marquis 1990, Metzger 1990, Gilliam and Turrill 1993). We considered it unlikely that boulders could provide such long-term suitable conditions because the layer of organic material on the surface of the boulders was shallow, uneven, and

prone to desiccation (Carson, pers. observation). Still, boulders may be habitats where competition from beech root sprouts is ameliorated. If so, then we would have expected to find a negative relationship between the abundance of beech and other woody species on the forest floor; we found no such relationship. We acknowledge that other mechanisms may promote understory species on boulders, including stunted tree growth that minimizes tree-herb competition, higher light levels on tall boulders, and greater habitat heterogeneity. Future research that quantifies light levels and heterogeneity between the boulders and the forest floor and explores the competitive relationships between trees, shrubs, and herbs would help to determine the validity of these alternative explanations. Regardless, we believe that the most parsimonious and obvious explanation for a greater density and species richness of trees, shrubs, and herbs on boulders was that boulders provided a refuge for these species, almost all of which are known to be vulnerable to deer browsing.

Our results add to the growing list of studies that demonstrate that too many deer can dramatically change patterns of abundance and species richness within forests thereby creating depauperate understory communities dominated by only those species capable of withstanding long-term and heavy deer browsing. Furthermore, abundant fern and beech in the understory could become inimical to both woody and herbaceous species alike and thus another future ob-

stacle to the regeneration of a species rich understory (Horsley and Marquis 1983; Drew 1990; Kolb et al. 1990; Lyon and Sharp 1995; George and Bazzaz 1999a,b; de la Cretaz and Kelty 1999). Overall, our study suggests that if deer numbers remain high, the future canopy of the ANF will be less diverse, be less even, contain less hemlock, red maple, yellow birch, and much more beech. This depauperate pattern of regeneration seems particularly troubling given the spread of beech bark disease throughout the ANF.

Can large boulders serve as a bioassay of the magnitude of overbrowsing in forests: Overcoming the ghost of herbivory past.

We propose that large boulders could serve as a cheap and efficient bioassay of deer damage to and impact on forest biodiversity and regeneration. Although this approach is not as rigorous as the use of replicated fenced areas that exclude deer, such fenced areas are expensive to build and maintain. Furthermore, if deer populations have been high for long periods of time, as in the Allegheny National Forest, then vulnerable species may be at very low abundance or even locally extirpated. If so, researchers and managers may have to exclude deer for years via fences to quantify the full magnitude of the effect of overbrowsing because natural and local seed sources of palatable species may be extremely low or absent. This problem will be exacerbated if vulnerable species are also poor dispersers (e.g., many herb species).

We term this problem the ghost of herbivory past and although speculative, we suggest that there will be a large lag time between the exclusion of deer (or management strategies that bring deer populations down) and an increase in the diversity and abundance of plant species vulnerable to browsing. Large boulders circumvent this problem because they were functioning as refugia throughout periods of high deer populations, and thus the plant communities on the surface of these large boulders may best reflect the vegetation before long periods of overbrowsing. Thus, boulders could be used in conjunction with fences

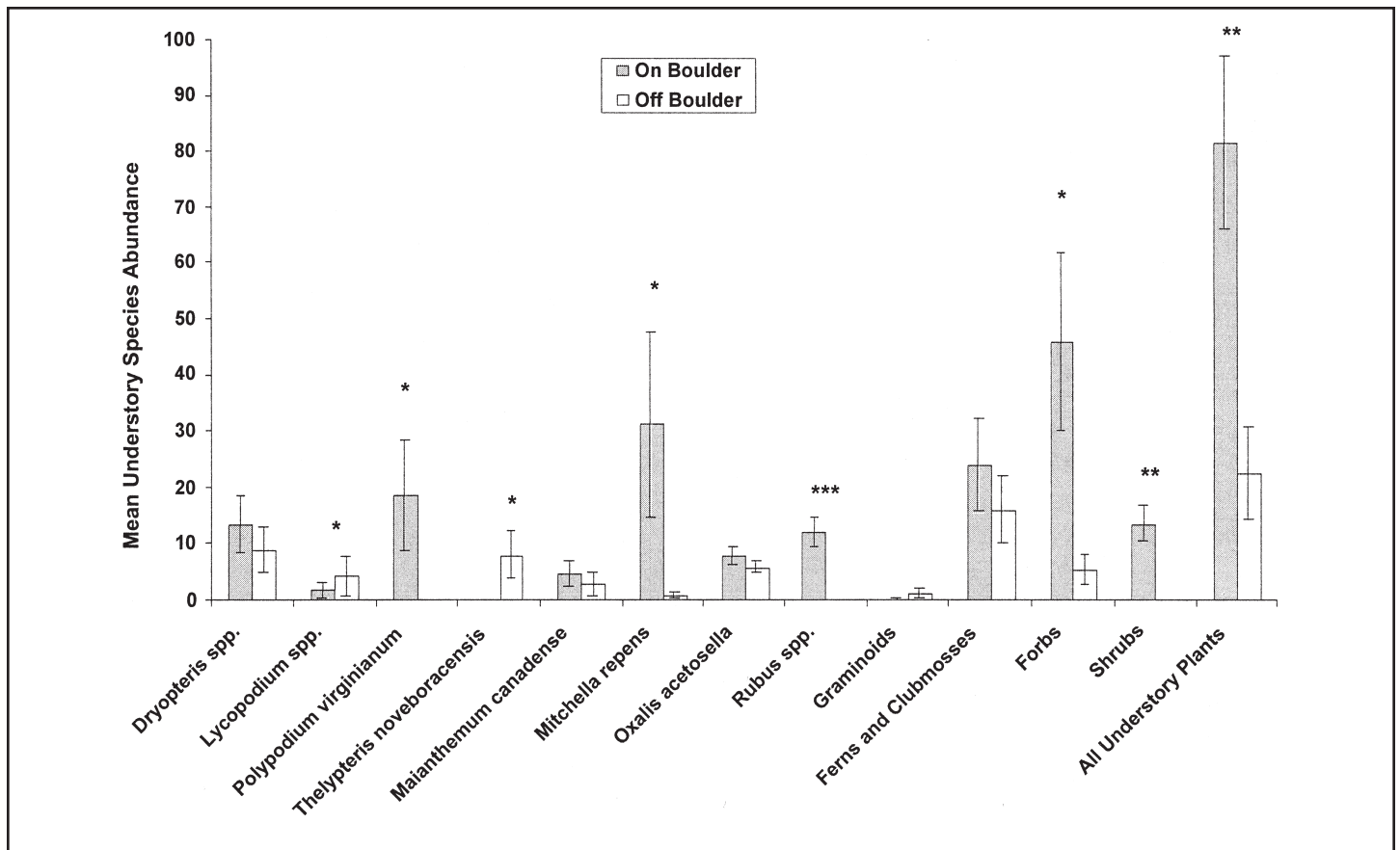


Figure 2. Mean percent cover of understory species on the surface of boulders and on the forest floor. The bars represent ± 1 standard error. No shrubs were found on the forest floor. The P-values are from paired t-test (* = <0.05 , ** = <0.01 , *** = <0.001).

to not only quantify the impact of deer but also to determine the length of the time it takes fenced plots to converge on the vegetation found on the surface of large boulders. Consequently, the magnitude of the ghost of herbivory past could be assayed. There are, of course, problems with this approach. For example, it is unclear how closely the vegetation of boulders matched the vegetation on the forest floor prior to long periods of overbrowsing both because of differences between boulders and forest floor and small population sizes on boulders leading to demographic stochasticity and random extinctions (see below). Nonetheless, forest managers and conservationists are going to have to be creative and use all means at their disposal to gauge the impact of deer overpopulation. Using boulders seems a logical and inexpensive approach both as a bioassay and as an educational tool.

How valuable are the refugia for the persistence of forest herbs?

It is conceivable that the herb and shrub communities on the surface of boulders could serve as source populations for the recolonization of the forest floor under lower deer pressure. The actual recolonization potential, however, could be less than anticipated. Forest herbs have short dispersal distances (Beattie and Culver 1981, Handel et al. 1981, Matlack 1994) and slow rates of reproduction and growth (Sobey and Barkhouse 1977, Bierzychudek 1982). Furthermore, many of these herbs appear susceptible to competition (Bratton 1976, Rogers 1983, Hughes 1992), and thus the spread of beech and fern species may be an added impediment. In addition, the area occupied by boulders is minimal (much less than 0.1% of the ANF) and these characteristically small and isolated populations are likely to have reduced vigor because of low levels genetic

diversity via genetic drift and inbreeding (Nei et al. 1975, Lande and Barrowclough 1987, Barrett and Kohn 1991, Rosquist and Prentice 2000). All these factors present formidable barriers to the survival and recolonization potential of these relict populations. Further research into these and other types of refugia may help clarify the role that these small, isolated populations would play in the subsequent spread of these vulnerable species if deer densities were ever reduced.

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LITERATURE CITED

- Alverson, W.S., D.M. Waller, and S.L. Solheim. 1988. Forests too deer: edge effects in northern Wisconsin. *Conservation Biology* 2:348-358.
- Anderson, R.C., and O.L. Loucks. 1979. White-tail deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. *Journal of Applied Ecology* 16:855-861.
- Antos, J.A. 1988. Underground morphology and habitat relationships of three pairs of forest herbs. *American Journal of Botany* 75:106-113.
- Augustine, D.J., and L.E. Frelich. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. *Conservation Biology* 12:995-1004.
- Balگووین, C.P., and D.M. Waller. 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. *Natural Areas Journal* 15:308-318.
- Barrett, S.C.H., and J.R. Kohn. 1991. Genetic and evolutionary consequences of small population size in plants: implications for conservation. Pp. 3-30 in D.A. Falk, and K.E. Holsinger, eds., *Genetics and Conservation of Rare Plants*. Oxford University Press, N.Y.
- Bauer, W.A. 1977. Forage Preferences of tame deer in the aspen type of northern Michigan. M.S. thesis, Michigan Technological University, Houghton.
- Beals, E.W., G. Cottam, and R.J. Vogl. 1960. Influence of deer on vegetation of the apostle islands. *Wisconsin Journal of Wildlife Management* 24:68-80.
- Beattie, A.J., and D.C. Culver. 1981. The guild of myrmecochores in the herbaceous flora of West Virginia forests. *Ecology* 62:107-115.
- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65:1406-1419.
- Bierzuchudek, P. 1982. Live histories and demography of shade-tolerant temperate forest herbs: a review. *New Phytologist* 90:757-776.
- Bjorkbom, J.C., and R.G. Larson. 1977. The Tionesta Scenic and Research Natural Areas. General Technical Report NE-31, U.S. Department of Agriculture, Forest Service, NE Forest Experiment Station, Upper Darby, Pa.
- Blair, R.M., and L.E. Brunett. 1980. Seasonal browse selection by deer in a southern pine-hardwood habitat. *Journal of Wildlife Management* 44:79-88.
- Bratton, S.P. 1976. Resource division in an understory herb community: responses to temporal and microtopographic gradients. *American Naturalist* 110:679-693.
- Collins, R.J., and W.P. Carson. 2003. The fire and oak hypothesis: incorporating the effects of deer browsing and canopy gaps. Pp. 44-63 in *Proceedings of the 13th Central hardwood Forest Conference*, April 1-3 2003, Urbana-Champaign Ill. Research Station General Technical Report, U.S. Department of Agriculture, Forest Service, North Central Research Station, St. Paul, Minn.
- De La Cretaz, A., and M.J. Kelty. 1999. Establishment and control of hay-scented fern: a native invasive species. *Biological Invasions* 1:223-236.
- Drew, A.P. 1990. Fern and aster effects on black cherry shelterwood regeneration. *Canadian Journal of Forest Research* 20:1513-1514.
- Erdmann, G.G. 1990. Yellow Birch. Pp. 133-147 in *Silvics of North America*, Volume II, R.M. Burns and B.H. Honkala, eds., *Agriculture Handbook 654*, U.S. Department of Agriculture, Washington, D.C.
- Fletcher, J.D., W.J. McShea, L.A. Shipley, and D. Shumway. 2001. Use of common forest forbs to measure browsing pressure by white-tailed deer (*Odocoileus virginianus* Zimmerman) in Virginia, USA. *Natural Areas Journal* 21:172-176.
- Gabriel, W.J., and R.S. Walters. 1990. Striped Maple. Pp. 53-59 in *Silvics of North America*, Volume II, R.M. Burns and B. H. Honkala, eds., *Agriculture Handbook 654*, U.S. Department of Agriculture, Washington, D.C.
- George, L.O., and F.A. Bazzaz. 1999a. The fern understory as an ecological filter: emergence and establishment of canopy-tree seedlings. *Ecology* 80:833-845.
- George, L.O., and F.A. Bazzaz. 1999b. The fern understory as an ecological filter: growth and survival of canopy-tree seedlings. *Ecology* 80:846-856.
- Gilliam, F.S., and J.L. Turrill. 1993. Herbaceous layer cover and biomass in a young versus a mature stand of a central Appalachian hardwood forest. *Bulletin of the Torrey Botanical Club* 120:445-450.
- Gleason, H.A., and A. Cronquist. 1991. *Manual of the vascular plants of Northeastern United States and adjacent Canada*, 2nd ed. New York Botanical Garden.
- Godman, R.M., and K. Lancaster. 1990. Eastern Hemlock. Pp. 604-612 in *Silvics of North America*, Volume I, R.M. Burns and B. H. Honkala, eds., *Agriculture Handbook 654*, U.S. Department of Agriculture, Washington, D.C.
- Grisez, T.J. 1960. Slash helps protect seedlings from deer browsing. *Journal of Forestry* 58:385-387.
- Handel, S.N., S.B. Fisch, and G.E. Schatz. 1981. Ants disperse a majority of herbs in a mesic forest community in New York State. *Bulletin of the Torrey Botanical Club* 108:430-437.
- Hill, J.D., and J.A. Silander. 2001. Distribution and dynamics of two ferns: *Dennstaedtia punctilobula* (Dennstaedtiaceae) and *Thelypteris noveboracensis* (Thelypteridaceae) in a northeast mixed hardwoods-hemlock forest. *American Journal of Botany* 88:894-902.
- Horsley, S.B. 1993. Mechanisms of interference between hay-scented fern and black cherry. *Canadian Journal of Forest Research* 23:2059-2069.

- Horsley, S.B., and D.A. Marquis. 1983. Interference by weeds and deer with Allegheny hardwood reproduction. *Canadian Journal of Forest Research* 13:61-69.
- Horsley, S.B., S.L. Stout, and D.S. deCalesta. 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecological Applications* 13:98-118.
- Hough, A.F. 1965. A twenty-year record of vegetational change in a virgin Pennsylvania forest. *Ecology* 46:370-373.
- Hughes, J.W. 1992. Effect of removal of co-occurring species on distribution and abundance of *Erythronium americanum* (Liliaceae), a spring ephemeral. *American Journal of Botany* 79:1329-1336.
- Johnson, S.A., P.E. Hale, W.M. Ford, J.M. Wentworth, J.R. French, O.F. Anderson, and G.B. Pullen. 1995. White-tailed deer foraging in relation to successional stage, overstory type, and management of southern Appalachian forests. *American Midland Naturalist* 133:18-35.
- Jones, R.H., and D.J. Raynal. 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). *American Journal of Botany* 73:1723-1731.
- Kolb, T.E., T.W. Bowersox, and L.H. McCormick. 1990. Influences of light intensity on weed induced stresses of tree seedlings. *Canadian Journal of Forest Research* 20:503-507.
- Korschgen, L.J., W.R. Porath, and O. Torgerson. 1980. Spring and summer foods of deer in the Missouri Ozarks. *Journal of Wildlife Management* 44: 89-97.
- Lande, R., and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pp. 87-124 in M.E. Soule, ed., *Viable Populations for Conservation*. Cambridge University Press, Cambridge, Mass.
- Lamson, N.I. 1990. Sweet Birch. Pp. 148-152 in *Silvics of North America, Volume II*, R.M. Burns and B. H. Honkala, eds., *Agriculture Handbook 654*, U.S. Department of Agriculture, Washington, D.C.
- Lay, D.W. 1969. Foods and feeding habits of white-tailed deer. *Proceedings of the white-tailed deer in Southern forest habitat symposium*, 25-26 March, Nacogdoches, Texas.
- Long, Z.T., W.P. Carson, and C.J. Peterson. 1998. Can disturbance create refugia from herbivores: an example with hemlock regeneration on treefall mounds. *Journal of the Torrey Botanical Society* 125:165-168.
- Lyon, J., and W.E. Sharp. 1995. Impacts of hayscented fern (*Dennstaedtia punctilobula*) and subsoil liming on the growth and nutrition of northern red oak (*Quercus rubra*) seedlings grown in multi-horizon forest soil miniterracosms. *Bulletin of the Ecological Society of America* 76:359.
- Magurran, A.E. 1988. *Ecological Diversity and Its Measurement*. Princeton University Press, Princeton, N.J.
- Marquis, D.A. 1975. The Allegheny hardwood forests of Pennsylvania: their bounty of timber and deer are the results of events that occurred many years ago. General Technical Report NE-15, U.S. Department of Agriculture, NE Forest Experiment Station. Broomall, Pa.
- Marquis, D.A. 1990. Black Cherry. Pp. 594-604 in *Silvics of North America, Volume II*, R.M. Burns and B. H. Honkala, eds., *Agriculture Handbook 654*, U.S. Department of Agriculture, Washington, D.C.
- Matlack, G.R. 1994. Plant species migration in a mixed-history forest landscape in eastern North America. *Ecology* 75:1491-1502.
- McCaffrey, K.R., J. Tranetzki, and J. Piechura Jr. 1974. Summer foods of deer in northern Wisconsin. *Journal of Wildlife Management* 38:215-219.
- McCullough, D.R. 1985. Variables influencing food habits of white-tailed deer on the George Reserve. *Journal of Mammalogy* 66:682-692.
- Metzger, F.T. 1990. American Hornbeam. Pp. 179-185 in *Silvics of North America, Volume II*, R.M. Burns and B. H. Honkala, eds., *Agriculture Handbook 654*, U.S. Department of Agriculture, Washington, D.C.
- Miller, S.G., S.P. Bratton, and J. Hadidian. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. *Natural Areas Journal* 12:67-74.
- Nei, M., T. Maruyama, and R. Chakraborty. 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29:1-10.
- Nixon, C.M., M.W. McClain, and K.R. Russel. 1970. Deer food habits and range characteristics in Ohio. *Journal of Wildlife Management* 34:870-886.
- Peterson, C.J., W.P. Carson, B.C. McCarthy, and S.T.A. Pickett. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58:39-46.
- Rogers R.S. 1983. Annual variability in community organization of forest herbs: effect of an extremely warm and dry early spring. *Ecology* 64:1086-1091.
- Rooney, T.P. 1997. Escaping herbivory: refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. *Journal of the Torrey Botanical Society* 124:280-285.
- Rooney, T.P., and W.J. Dress. 1997. Species loss over sixty-six years in the ground-layer vegetation of heart's content, an old-growth forest in Pennsylvania, USA. *Natural Areas Journal* 17:297-305.
- Rosquist, G., and H.C. Prentice. 2000. Habitat fragmentation and the structure of genetic diversity within disjunct isolates of *Anthriscum ramosum* L. (Anthericaceae) in Scandinavia. *Biological Journal of the Linnean Society* 69:193-212.
- Russell, F.L., D.B. Zippin, and N.L. Fowler. 2001. Effects of white-tailed deer (*Odocoileus virginianus*) on plants, plant populations and communities: a review. *American Midland Naturalist* 146:1-26.
- Sauer, P.R., J.E. Tanck, and C.W. Severinghaus. 1969. Herbaceous food preferences of white-tailed deer. *New York Fish and Game Journal* 16:145-157.
- Schopmeyer, C.S. 1974. Seeds of woody plants in the United States. *Agriculture Handbook 450*, U.S. Department of Agriculture, Washington, D.C.
- Skinner, W.R., and E.S. Telfer. 1974. Spring, summer, and fall foods of deer in New Brunswick. *Journal of Wildlife Management* 38:210-214.
- Sobey, D.G., and P. Barkhouse. 1977. The structure and rate of growth of the rhizomes of some forest herbs and dwarf shrubs of New Brunswick-Nova Scotia border region. *Canadian Field Naturalist* 91:377-383.
- Sotala, D.J., and C.M. Kirkpatrick. 1972. Foods of white-tailed deer, *Odocoileus virginianus*, in Martin County, Indiana. *American Midland Naturalist* 89:281-286.
- Stiteler, W.M., Jr., and S.P. Shaw. 1967. Use of woody browse by white-tailed deer in heavily forested areas of northeastern United States. *Transactions North American Wildlife and Natural Resources Conference* 31:205-212.
- Stoeckler, J.H., R.O. Strothmann, and L.W. Kreftint. 1957. Effect of deer browsing on reproduction in the northern hardwood-hemlock type in the northeastern Wisconsin. *Journal of Wildlife Management* 21:75-80.
- Stormer F.A., and W.A. Bauer. 1980. Summer forage use by tame deer in northern Michigan. *Journal of Wildlife Management* 44:98-106.
- Sundquist, B., C.W. Yartz, and J. Richardson. 1990. *Allegheny National Forest Hiking Guide*, 3rd ed., Allegheny Group, Sierra Club. Pittsburgh, Pa.
- Tilghman, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53:524-532.

-
- Waller, D.M., and W.S. Alverson. 1997. The white-tailed deer: a keystone herbivore. *Wildlife Society Bulletin* 25:217-226.
- Webb, W.L., R.T. King, and E.F. Patric. 1956. Effect of white-tailed deer on a mature northern hardwood forest. *Journal of Forestry* 54:391-398.
- Webster, C.R., and G.R. Parker. 2000. Evaluation of *Osmorhiza claytonii* (Michx.) C.B. Clarke, *Arisaema triphyllum* (L.) Schott, and *Actaea pachypoda* Ell. As potential indicators of white-tailed deer overabundance. *Natural Areas Journal* 20:176-188.
- Webster, C.R., M.A. Jenkins, and G.R. Parker. 2001. A field test of herbaceous plant indicators of deer browsing intensity in mesic hardwood forests of Indiana, USA. *Natural Areas Journal* 21:149-158.
- Whitney, G.G. 1984. Fifty years of change in the arboreal vegetation of Heart's Content, an old-growth hemlock-white pine-northern hardwood stand. *Ecology* 65:403-408.
- Whitney, G.G. 1990. The history and status of the hemlock-hardwood forests of the Allegheny Plateau. *Journal of Ecology* 78:443-458.