Forests Too Deer: Edge Effects in Northern Wisconsin

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Abstract: *Browsing by white-tailed deer (*Odocoileus virginianus*) can profoundly affect the abundance and population structure of several woody and herbaceous plant species. Enclosure studies and population surveys reveal that past and current deer densities as low as 4 deer/km^2 may prevent regeneration of the once common woody species, Canada yew (*Taxus canadensis*), eastern hemlock (*Tsuga canadensis*), and white cedar (*Thuja occidentalis*), as well as several herbaceous species. Prior to European settlement, forests in northern Wisconsin contained relatively sparse deer populations (<4/km^2), but extensive timber cutting in the late nineteenth century boosted deer populations. Continued habitat fragmentation resulting from scattered timber harvests and the creation of "wildlife openings" to improve deer forage maintain these high densities throughout much of the Northeast.*

Because deer wander widely, the effects of high deer densities penetrate deeply into remaining stands of old and mature forest, greatly modifying their composition. Thus, abundant early successional and "edge" habitat, and the high deer densities they engender, represent significant external threats

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Resumen: *El pastoreo y ramoneo del venado de cola blanca (*Odocoileus virginianus*) en la zona norteña del estado de Wisconsin, puede afectar profundamente a la abundancia y estructura de población de varias especies de plantas herbáceas y leñosas. Antes de la Colonia, los bosques norteños de Wisconsin eran habitat de poblaciones relativamente pequeñas de venados (menos de 4 por Km^2) pero las extensas talas de estos bosques, a finales del siglo 19, dió paso a un incremento poblacional de estas especies. Estudios recientes de unidades de exclusión y catastros poblacionales revelan que, en efecto, una densidad de solo 4 ejemplos por Km^2 logra impedir la regeneración de las especies de* Taxus canadensis, Tsuga candensis *y* Thuja occidentalis, *muy conocidas otrora, como tambien varias especies herbáceas. La fragmentación de habitats, que ha resultado de la tala dispersa de arboles y la creación, de "claros silvestres" con propósitos de incrementar el forraje para los venados, ha aumentado las poblaciones de estas especies a lo largo de la región del nordeste.*

Debido a que un gran número de venados vagan ampliamente en la región, los efectos sobre los espacios remanentes de bosque maduro son considerables modificandose significativamente su composición. De esta manera, incipientes y extensos ecotonos, ademas de las grandes densidades de poblaciones de venados que estos albergan, representan una amenaza externa sobre estas comunidades de bosque.

to these plant communities. We hypothesize that establishing large (200–400 km²) continuous areas of maturing forest, especially in conjunction with increased hunting, could reduce local deer densities and so provide a simple and inexpensive method for retaining species sensitive to the deleterious effects of browsing.

Nos permitimos suponer que el establecimiento de grandes y continuas áreas de bosques en desarrollo (200–400 Kms), conjuntamente con el incremento en la actividad de caza, podría reducir localmente la densidad de población de los venados y de esta forma disponerse de un método simple y poco costoso que permita conservar estas expecies sujetas al deterioro por efectos del pastoreo y ramoneo.

> [M]obile animals greatly affect plant life, so that a small virgin forest may *appear* to be natural when actually it has been profoundly affected by forces applied to animals, waters, or climate at points far distant. (Thus the deer populations determined by laws passed at Lansing, by hunters . . . , and by lumbering operations . . . have apparently exterminated the ground hemlock [yew] from the "virgin" forest of Mountain Lake.)
>
> A. Leopold (1938)

Ever since the pioneering work of Leopold (1936) on habitat manipulation, wildlife biologists have strived to boost populations of game species by creating clearings and other areas of sharp transition between two or more types of plant community. Indeed, the traditional meaning of the term "edge effect" was the local increase in the diversity and abundance of animal species found along the boundary between two habitat types (Leopold 1936; Swift 1946; Dahlberg & Guettinger 1956; Yahner 1988). In seeking to explain this phenomenon, a number of other edge effects have been noted, including microclimatic changes in temperature, light, and humidity; altered tree species composition due to increased colonization by shade-intolerant and exotic plants; invasions by insects; and increased parasitism, predation, and competition by "weedy" birds and mammals (Ranney, Bruner, & Levenson 1981; Matthiae & Stearns 1981; Guntenspergen 1983; Brittingham & Temple 1983; Wilcove 1985; Janzen 1983, 1986; Wilcove, McLellan, & Dobson 1986; Yahner & Scott 1988).

Because the apparently beneficial effects of habitat tend to be local (on the order of a few hundred meters at most), wildlife managers often try to establish small clearings throughout a forested area. These efforts, the simultaneous creation of edge via other ongoing human disturbances, and controls on hunting have resulted in abundant populations of game and other edge-loving species. As reflected in the leading quote, however, some naturalists recognize a darker side to edges. Within conservation biology, the term "edge effects" is now usually used to refer to increased predation and parasitism of vulnerable animals in the vicinity of edges (e.g., Temple & Cary 1988). We would like to extend this connotation to include the deleterious effects of herbivores on sensitive plant species within stands of mature forest. While younger forest can undoubtedly buffer older forests against many microclimatic and biological edge effects (as assumed for western U.S. forests by Harris 1984), such a matrix might also threaten diversity by facilitating the invasion of successional plants and animals capable of interfering with species restricted to older communities (Janzen 1983, 1986).

Here, we review evidence that herbivory can profoundly alter plant community composition in the Northeast. We became concerned that such efforts could be widespread after learning of Hough's (1965) 20-year field study in the Allegheny National Forest in Pennsylvania, where he found the understory of a large (1650 ha) tract of virgin hemlock-hardwood forest to be severely damaged by deer browsing. Because herbivorous mammals wander widely and can invade even areas of ostensibly unfavorable habitat, such edge effects penetrate much farther than those previously reported for the region. This raises the important policy question of how plant species diversity is to be retained in areas subject to regional management for high deer densities. For concreteness and relevance, we primarily discuss interactions between white-tailed deer (*Odocoileus virginianus*) and various plants in northern Wisconsin (scientific names in Table 1). Policy decisions are now pending regarding this issue in two National Forests located there (Task Force 1986; U.S. Forest Service 1986).

The Context: Northern Wisconsin

Land survey records and detailed analyses of remnant forest stands allow a reasonable reconstruction of presettlement forest conditions (Curtis 1959; Finley 1976). Upland mesic forest habitats were predominantly old-growth (200–300 years old), with only 17–25% of their area occupied by successional communities (Canham & Loucks 1984). This relationship has now been reversed, with small patches of old and mature growth occupying less than 5% of the forest within a matrix of younger successional communities. The pre-Columbian forest contained about 64% "hardwood" by area and consisted mostly of the hemlock-hardwood community type. Intact, mature examples of this forest type are now relegated to token occurrence, primarily in existing or proposed "Research Natural Areas" 12 to 260 ha in size.

Because white pine, once a major component of northern Wisconsin forests, was preferred by early loggers, its abundance was drastically reduced. Hemlocks were then cut preferentially to service the tanning trade. Finally, with increasing demand for hardwood

Table 1. Common and scientific names of organisms mentioned in the text.

Aspen	*Populus tremuloides* Michx.
Black ash	*Fraxinus nigra* Marsh.
Blunt-leaved orchid	*Habenaria obtusata* (Pursh) Richards.
Buckthorn	*Rhamnus cathartica* L.
Flowering dogwood	*Cornus florida* L.
Hemlock, eastern hemlock	*Tsuga canadensis* (L.) Carr.
Honeysuckle	*Lonicera tatarica* L., *L. morrowi Gray, and their hybrid, L.* X *bella* Zabel
Indian cucumber-root	*Medeola virginiana* L.
Large-flowered trillium	*Trillium grandiflorum* (Michx.) Salisb.
Leatherwood	*Dirca palustris* L.
Purple fringed orchid	*Habenaria psycodes* (L.) Spreng.
Redbud	*Cercis canadensis* L.
Showy lady's-slipper orchid	*Cypripedium reginae* Walt.
Sugar maple	*Acer saccharum* Marsh.
Tall northern bog orchid	*Habenaria hyperborea* (L.) R. Br.
Yellow birch	*Betula alleghaniensis* Britton
Yew, Canada yew, ground hemlock	*Taxus canadensis* Marsh.
Yew-tree	*Taxus baccata* L.
White cedar	*Thuja occidentalis* L.
White oak	*Quercus alba* L.
White pine	*Pinus strobus* L.
Wood sorrel	*Oxalis acetosella* L.
Yellow lady's-slipper orchid	*Cypripedium calceolus* L.
Brainworm	*Parelaphostrongylus tenuis*
Canadian lynx	*Lynx canadensis* Kerr
Deer, white-tailed deer	*Odocoileus virginianus* (Zimmerman)
Deer tick	*Ixodes*
Elk, American elk	*Cervus elaphus* Linnaeus
Moose	*Alces alces* (Linneaus)
Mountain lion	*Felis concolor* Linnaeus
Timber wolf	*Canis lupus* Linnaeus
Wolverine	*Gulo gulo* (Linnaeus)
Woodland caribou	*Rangifer tarandus* (Linnaeus)

during and after World War I, most of the area was clearcut. Wisconsin's two National Forests, the Chequamegon and Nicolet, were created in the 1920s and 30s and now occupy 3,420 and 2,650 km^2, respectively (Fig. 1).

Aspen is the preeminent early successional tree species of the region. Its wind-dispersed seeds, clonal propagation, and fast growth allow it to quickly occupy large areas. Partly because it freely root-sprouts following fire or cutting, it has increased from about 1% on these National Forests presettlement to about 26% now (U.S. Forest Service 1986*c*). Other disturbance and edge-adapted species were originally rather scarce and limited to tree-fall gaps, riparian habitats, and areas of forest recently blown down or burned. They are now quite

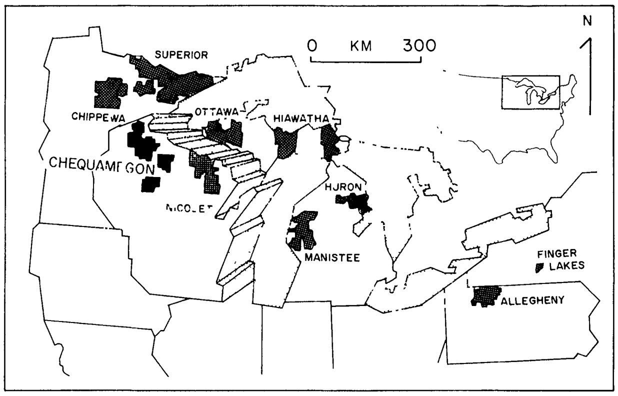

Figure 1. The U.S. National forests of the Great Lakes region. Stippled areas represent the Great Lakes and solid lines the boundaries between states. The Chequamegon and Nicolet National Forests of northern Wisconsin are 3,420 and 2,650 km^2, respectively. Source: Modified from U.S.D.A. Forest Service map.

common throughout these forests. Many weedy, exotic plant species have colonized heavily disturbed habitats, but the less disturbed habitats have not yet been seriously invaded (unlike the situation in southern Wisconsin, where buckthorn and honeysuckle have invaded even "intact" forests [Barnes & Cottam, 1974]).

Not surprisingly, major changes in Wisconsin's fauna have also occurred during the last century. Moose, elk, and woodland caribou, as well as predators like the wolverine, have all been extirpated. Forest disturbance does not fully explain why these species were lost, but is certainly a contributing factor (Jackson 1961; Gates, Clarke, & Harris 1983). Timber wolf and Canadian lynx continue to occupy sections of both forests but are quite scarce, largely due to human activity. Although it was assumed to be extirpated, there have been several recent sightings of the mountain lion (Lewis & Craven 1987).

Population Densities of Deer

Severe winters and wide expanses of virgin timber lacking undergrowth originally produced marginal habitat for the white-tailed deer in the northern Great Lakes region (Swift 1946; Schorger 1953; Dahlberg & Guettinger 1956, Blouch 1984; but see Habeck & Curtis 1959). As stated by the U.S. Forest Service, "Species associated with aspen and other early successional stages were present but in low numbers. Early settler's notes indicate few deer and other game animals in northern Wisconsin" (1986*c*, p. D5).

Deer populations in northern Wisconsin were originally less than 4/km^2 of range, and probably as low as

$2/km^2$ over large areas of range (total surface area minus the area of lakes, rivers, urban areas, and large farms). Populations began to rise in the mid-1850s and peaked in the Forest in the 1930s and 1940s at about $14/km^2$ due to extensive favorable habitat and protective hunting laws (Swift 1946; Dahlberg & Guettinger 1956; McCaffery 1986). During the last 25 years, densities in northern Wisconsin have ranged from 5 to $12/km^2$ (McCaffery 1986) and are now estimated at 2 to 9 deer/km^2 in the northern units of Wisconsin's National Forests (F. Haberland, personal communication, data for 1985 and 1986). The stated goals of the Forest Service for deer production are much higher, calling for sufficient habitat to support 31,952 deer in the Chequamegon, or 9.3 deer/km^2 (U.S. Forest Service 1986*a*, p. B4). Goals of the Wisconsin Department of Natural Resources are for 4 to 8 deer/km^2 overwintering in the same area (F. Haberland, personal communication).

Habitat management for deer in the Upper Great Lakes region entails establishing winter range, young aspen growth, oaks for acorns, and openings in the forest to supply grasses and other pasturage (McCaffery 1984, 1986). In keeping with these traditional management practices, the management plans for the national forests intersperse small (<20 ha) timber cuts and openings designed to boost deer and other game populations throughout both Forests (U.S. Forest Service 1986). Collectively, these comprise at least 14% of the Forests' areas and should result in a uniform, abundant distribution of deer, a goal explicitly embraced by the Forest Service (Task Force 1986).

Effects of Deer Browsing on Woody Plants

The damage deer do to crop and natural vegetation has been extensively studied, and depends on deer density. High deer populations slow the regeneration of several commercial species, causing significant economic losses (Graham 1954; Marquis 1981; Redding 1987). However, as deer densities in northern Wisconsin have declined to levels below that which threatens commercial forestry or deer range per se, concern for deer damage to vegetation has virtually disappeared (McCaffery 1986).

Partial lists of preferred deer foods in Wisconsin all agree that Canada yew, eastern hemlock, and white cedar are highly preferred by deer during winter months (DeBoer 1947; Swift 1948; Cottam & Curtis 1956; Dahlberg & Guettinger 1956; Beals, Cottam, & Vogl 1960). Yew is severely damaged by deer because it is both sought out and does not recover well after browsing. For some time, there has been little or no reproduction of yew in most of the region (Stearns 1951; Curtis 1959) with many populations now lost from known sites of prior occurrence. Surviving populations exist on rocky outcrops that are inaccessible to deer, or as scattered individuals browsed nearly to ground level. The only other area in Wisconsin where yew populations are known to be extensive and healthy is in the tribal lands of the Menominee Reservation (Waller et al., in prep.) where year-round hunting limits deer densities (see below). On the nearby Apostle Islands in Lake Superior, Beals, Cottam, & Vogl (1960) found yew common on islands with few or no deer, yet yew were lacking in mainland forests. Leuthold (1980) has shown a similar decline of the related yew-tree in Switzerland and predicts extirpation of the species unless active protection occurs. Besides direct browsing losses, Canada yew suffers indirectly via a novel mechanism that has only recently been recognized: browsing skews floral sex ratios which, in turn, limit the availability of pollen to the point where it becomes limiting and reproduction is impaired (Allison 1987).

Like yew, eastern hemlock and white cedar are quite sensitive to deer browsing. Although these trees are capable of growing tall enough to escape browsing, deer can severely impair reproduction by preventing seedling and sapling recruitment, particularly since slow-growing seedlings and saplings of these species are vulnerable to browsing for decades (Hough 1965; Rogers 1978). Browsing is particularly conspicuous within winter deer yards in Wisconsin where hemlock and white cedar are reproducing poorly or not at all (Task Force 1986).

Deer enclosure studies carried out in Wisconsin, through other parts of the Northeast, and elsewhere show dramatic differences in survival and reproduction of hemlock, yew, white cedar, and other species within fenced enclosures compared to exposed individuals outside the protected areas (Graham 1954; Dahlberg & Guettinger 1956; Stoeckeler, Strothman, & Krefting 1957; Marquis 1974; Blewett 1976; Kroll, Goodrum, & Behrman 1986; Tilghman, in press; Fig. 2). These observations all support the results of Goff (1967), Anderson & Loucks (1979), and Waller et al. (in prep.), in which hemlock only exhibits a healthy population structure within Wisconsin on certain islands, in the Menominee Reservation, and within deer enclosures. Similar results hold for white cedar (Blewett 1976 and references therein), with striking differences in stem height and density within and outside enclosures.

The enclosure illustrated contains a population of hemlock with hundreds of individuals representing all seedling and sapling age classes, yet the surrounding area outside the enclosure contains only a few individuals, which either show signs of recent browsing or are shorter than the winter snow cover. Nearby, a showcase grove of old-growth hemlocks is virtually devoid of recent hemlock reproduction, despite falling within a deer management unit with a reported population density of only 2 deer/km^2. Its understory is composed mainly of

Figure 2. Deer enclosure at Fould's Creek, Chequamegon National Forest, Wisconsin, viewed from the top of the 4 m high fence, which bisects the photograph. Vigorous growth of hemlock can be seen within the forty-year-old enclosure (left side of photograph). Source: W. S. Alverson, February, 1988.

stunted, gnarled sugar maple seedlings and saplings bearing the distinctive mark of heavy browsing by deer (cf. Fig. 1 in Switzenberg, Nelson, & Jenkins 1985; Fig. 1 in Stoeckeler, Strothman, & Krefting 1957).

Some researchers question whether deer browsing alone has caused the conspicuous changes in hemlock reproduction in the upper Midwest (Webb, King, & Patric 1956; Tierson, Patric, & Behrend 1966). Stearns (1951) suggested that changes in climate or catastrophic storms allowed greater hemlock regeneration during certain periods in the past (reviewed by Eckstein 1980). This seems unlikely, however, both from the enclosure studies cited above and because cycles of hemlock reproduction are asynchronous between noncontiguous stands and appear to be governed by internal stand dynamics (Hett & Loucks 1976).

Even more definitively, Frelich & Lorimer (1985) documented changes in size-class distributions and extensive browse damage to young hemlock that appear directly attributable to deer browsing in the Porcupine Mountains of Michigan's Upper Peninsula. A forest near the Lake Superior shore with an estimated deer density of $10/km^2$ (winter) suffered almost complete annihilation in some size classes, while inland sites with lower winter deer densities ($2/km^2$) exhibited unimpaired reproduction. They rejected the hypothesis that climate was responsible for the differences in hemlock reproduction by demonstrating that herbivory was the causal factor. A model they constructed predicts eventual exclusion of hemlock by hardwood species in the coastal sites within 200 years if deer densities remain high.

In a study designed specifically to test whether high deer densities prevent reproduction in these species, we compared hemlock's population structure within the Menominee Reservation to its structure within the adjacent Nicolet National Forest (Waller et al., in prep.). Because the Menominee Reservation allows hunting year-round, deer densities are lower than in surrounding areas (ca. $1–2/km^2$; Morehouse & Becker 1966; O. Rongstad, personal communication). While almost half of the stands within the Menominee showed substantial hemlock reproduction, less than 6% of those in the Forest did. The Nicolet stands exhibit drastically reduced seedling abundance, especially relative to the number of adult trees (Fig. 3).

Other Species Affected by High Deer Densities

Deer can affect the composition of entire communities and not just individual woody plant species. For example, in Great Smoky Mountains National Park, areas subject to intensive deer browsing close to openings lost

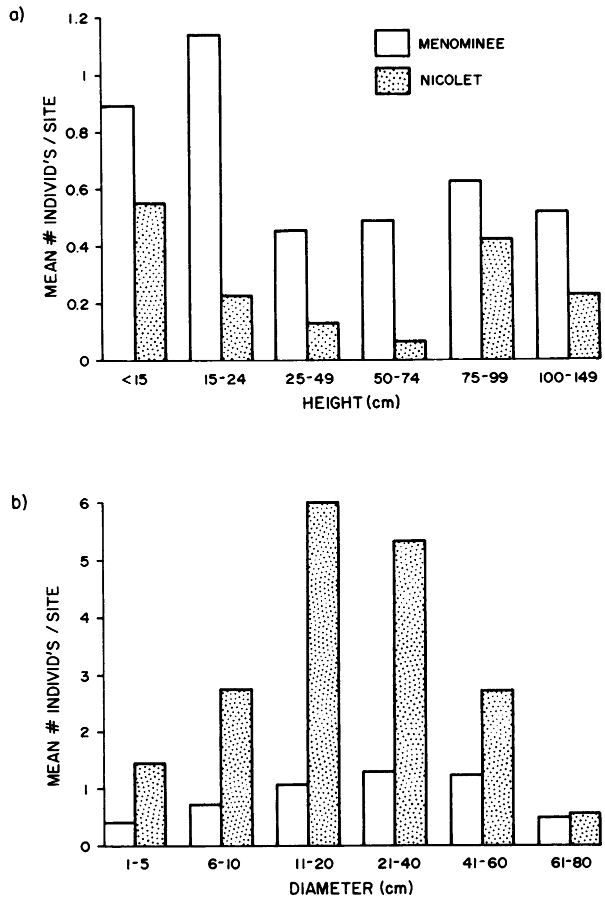

Figure 3. Size distributions of eastern hemlock seedlings (a) and adult trees (b) in the Menominee Reservation and the adjacent Nicolet National Forest. Deer densities are much lower in the Menominee Reservation due to year-round hunting. Source: Data from Waller, Judziewicz, Alverson, & Solheim (in prep.).

more than a quarter of their total species richness compared to control areas (Bratton 1979). White oak, redbud, and flowering dogwood all appeared to be significantly affected by deer browsing. Not just plant species are affected, either. Moose are thought to be excluded from many areas by infection with brainworm, a parasite carried by deer. Decreases in deer abundance could enhance the chances for immigrant moose now drifting into northern Wisconsin to become successfully reestablished, as recently occurred in New York (Hicks & Stumvoll 1985). Lyme disease, carried primarily by deer ticks, also appears to be increasing in many areas in response to increased deer abundance, but no effects on animal communities are yet evident.

Many herbaceous species are also favored by deer, including the showy and yellow lady's slipper orchids, the blunt-leaf orchid, the tall northern bog orchid, and the purple fringed orchid. Many of these could be experiencing reduced reproductive success and/or local extirpation due to intensified deer herbivory (Cottam & Curtis 1956; L. Lipsey, personal communication; personal observation). Enclosure studies in the Allegheny National Forest of northwestern Pennsylvania demonstrated that deer populations of 4/km^2 caused significant reductions in the abundance of Indian cucumber-root and large-flowered trillium, both of which also occur in northern Wisconsin (Tilghman, in press). Like yew, herbs are highly susceptible to herbivory by deer because they never outgrow the zone of accessibility (approximately 2 m).

Changes in canopy composition could also result in changes in community composition in other forest strata. For example, observed and predicted losses of mature hemlock and other northern hardwood canopies in the Forest could cause the eventual loss of shrubs and herbs like leatherwood and wood sorrel that tend to be restricted to these habitats (Stearns 1951; personal observation). As evergreen conifers lose dominance to deciduous species like sugar maple and black ash, light regimes change drastically and understory species can be expected to respond. Furthermore, as remaining habitats of older hemlock and white cedar become smaller and more isolated, further gradual but inexorable losses of the many species restricted to these habitats are expected via "relaxation" (MacArthur & Wilson 1967). How quickly this occurs obviously depends on species-specific characteristics, but analogous losses of herb species have been documented for isolated forests in southern Wisconsin (Hoehne 1981).

Recommended Deer Densities

Assuming that deer browsing has caused the observed reductions in reproduction of hemlock, yew, and white cedar, it becomes important to determine that density of deer below which successful regeneration is possible. While few studies directly addressing this question exist, existing work allows us to infer which densities are clearly incompatible with successful reproduction. For example, studies of deer carrying capacity routinely suggest that densities of 8 deer/km^2 are compatible with good range management. However, studies of carrying capacity are normally undertaken out of primary concern for healthy populations of deer or commercial timber species, especially their ability to fulfill their auxiliary role as "cover" or "browse" for deer. Such studies provide little or no assurance that the impact of deer is uniformly benign. For example, Tubbs, Jacobs, & Cutler (1983) combine data for hemlock with numerous other species composing the "northern hardwood types," and obscure the problematic relationship with deer: "The northern hardwood types can support relatively high populations of deer without serious injury; damage will be minimal if management practices favor dense reproduction and vigorous shoot growth (Jacobs 1969)" (p. 122). Yet Jacobs considers only the ability of sugar maple to survive under such deer densities, not hemlock, yellow birch, or yew, all important components of the northern hardwood forest. Furthermore, it is sugar maple that replaces hemlock in this region as the latter is browsed (Anderson & Loucks 1979; Frelich & Lorimer 1985).

Densities of 8/km^2 appear far too high if maintaining the diversity of all plants and animals is the management objective, as reviewed above. Instead, deer densities approximating presettlement conditions for substantial periods of time appear necessary to ensure the survival and healthy reproduction of hemlock, yew, and other sensitive plant species. Existing meager data suggest this density to be less than 4 deer/km^2, and possibly as low as 1–2 deer/km^2. Precise figures cannot yet be stated because of the lack of thorough, species-specific studies in our region. A wildlife biologist currently studying deer movements in the area suggests that young hemlock occur in areas where deer densities approach 2/km^2 (O. Rongstad, personal communication).

Discussion

Browsing by elevated populations of white-tailed deer appears to constitute a major edge effect in the forests of northern Wisconsin and perhaps other parts of the Northeast. Deer affect forest composition through direct, well-documented negative effects on several woody plant species and through direct and indirect damage to many herbaceous species. Failure to acknowledge these ecological interactions and plans to maintain dense populations of deer (8–9.3/km^2) by state and federal land stewards work directly against the preservation of these components of natural diversity.

What steps could be taken to protect the viability of species sensitive to browsing at high deer densities? Habitats suitable for deer-sensitive species could be created in at least three ways: enclosures, increased hunting, or habitat management to reduce deer densities. Other means of controlling deer density exist (such as deer repellents and birth control), but these are unlikely to be viable solutions (Redding 1987; Marquis 1987).

Enclosures are now being used in northwestern Pennsylvania for regenerating commercial forest stands (Marquis 1987), but are extremely expensive to construct and maintain (Kochel & Brenneman 1987; U.S. Forest Service 1986c, p. F63). Alternatively, commercial seedling caps can be used to protect individual seedlings, also at great cost. Both enclosures and seedling protectors appear best suited to regenerate small local stands of a single target species such as hemlock or yew. However, such a solution, unless extended to a complete set of other sensitive plant species (many of which must still be unknown), offers no general relief. The same problem applies to the use of silvicultural techniques aimed at regenerating single species (Eckstein 1980; Johnson & Booker 1983; Tubbs, Jacobs, & Cutler 1983; Wendel et al. 1983; Marquis 1987). Such methods for hemlock require soil scarification, removal of litter, fencing and/or partial canopy removal while reducing the area's attractiveness to deer. These intrusive management techniques are prohibitively expensive on a large scale and could still cause or permit damage to other species sharing the habitat. It would also be an obvious mistake to assume that protecting hemlock (or any other particular species) somehow protects the overall diversity of the hemlock-hardwood forest community. At present, there exists neither the knowledge nor the will to create active programs of species-specific management for all deer-sensitive species in these communities.

Increased hunting pressure can also decrease deer populations locally (Morehouse & Becker 1966; Creed et al. 1984). While some uncertainty exists as to the relative importance of hunting versus deer behavior and habitat quality in determining deer population levels (McCaffery 1986), few doubt that increased hunting pressure would reduce browsing, especially if coupled with habitat alteration. Whether hunting alone could reduce deer densities to 2/km^2 is unclear, however, particularly since most hunters prefer to hunt in areas of known high deer density.

Species sensitive to high deer densities could also be protected by habitat management if vegetation capable of supporting only reduced deer densities could be established. This would involve running conventional game management practices in reverse. Instead of increasing edge habitat and young browse, large blocks of forest would be allowed to mature naturally to the point where they become inferior deer habitat (Fig. 4). Such

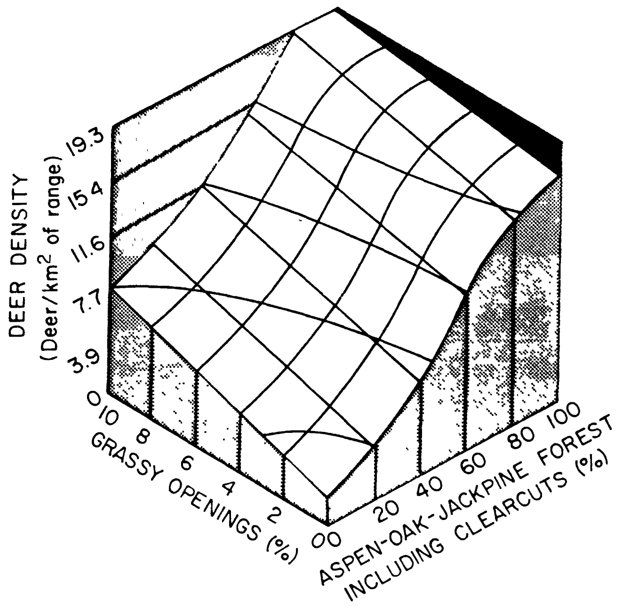

Figure 4. Theoretical model of the influence of habitat on the population densities of white-tailed deer in northern Wisconsin. Units of deer density, originally given in deer/mi^2, have been converted to deer/km^2; density figures are comparable to those given in the text. One purpose of Diversity Maintenance Areas would be to create large blocks of habitat corresponding to the lowermost surface of the slope. Source: Modified with permission from McCaffery (1986).

areas would have to be large and continuous enough to create core areas relatively free of the edge effects produced by deer and could be created by redistributing management activities in public (and perhaps private) forests. For example, efforts to harvest timber and improve deer habitat could be confined to 80% of each National Forest, leaving 20% in one or two large, contiguous blocks that would eventually become, through natural succession, habitats unfavorable to dense deer populations. This, in fact, represents the actual recommendation made in a formal appeal process involving Wisconsin's National Forests (Task Force 1986). The proposed biotic reserves were termed "Diversity Maintenance Areas."

The crucial question concerning this final alternative lies with size: How large must a block of old forest be to effectively reduce deer densities? The literature on deer movements is extensive but insufficient by itself to resolve the size issue (e.g., Tierson et al. 1985). Winter ranges of individual deer tend to be less than 480 ha in Minnesota (Rongstad & Tester 1969), with summer home ranges somewhat larger. Winter to summer range movements for adult deer averaged 5.6 km in a Wisconsin study, with 90% of the deer moving 12 km or less (Dahlbert & Guettinger, 1956). An eight-year study in

Michigan's Upper Peninsula found that the mean annual dispersal distance between winter yards and the following November kill site was 13.8 km for hunter-killed deer; yearly mean distances ranged from 10.9 to 20.2 km (Verme 1973). Bratton (1979) concluded that intensive deer impacts did not extend beyond 1 km away from openings in the Cades Cove region of Great Smoky Mountains National Park. Fortunately, a study on deer movements within the Forest is now underway (O. Rongstad, personal communication).

If we apply the average travel distance for deer of 8 km used by the Forest Service in its management plan (Task Force 1986), blocks of unfavorable habitat with radii of 8 km, constituting areas of ca. 200 km^2, might serve to halve deer densities at their center points. If unfavorable habitat like old growth is found to reduce travel distances, smaller areas might suffice. Prudence would dictate the conservative course of first designating larger areas, then reducing them if penetrations were found to be of shorter range. If the mean dispersal distance were reduced to 2 km in a circular block of unfavorable habitat, the block would still need to have a radius of 7 km to have a 1:1 ratio of edge to interior habitat. Historical patterns of movement and other particular features of deer behavior also clearly influence how such habitat blocks would function (Tierson et al. 1985). Such information is limited, making it difficult to predict *a priori* exactly how large the blocks of unfavorable habitat need to be to protect sensitive species.

Mature or old-growth forest blocks of this scale are much larger than any existing old-growth areas in northern Wisconsin. The two congressionally designated wilderness areas in the Chequamegon National Forest are 1,710 and 2,660 ha in size, comparable in size to Hough's (1965) 1,650 ha severely damaged study area in Pennsylvania. These wilderness areas are imbedded in a matrix of young forest containing extensive deer habitat. As more forest lands in northern Wisconsin mature, deer densities should decline slowly (McCaffery 1986). However, the National Forest plans call for increased timber harvests, which all convert nearly 50% of their area into new successional habitats during the next 50 years. This makes it unlikely that the wilderness areas will experience consistently low herbivory by deer over the foreseeable future, even when the wilderness areas themselves become old. In fact, the scattered, shifting pattern of timber harvests and the creation of additional "wildlife openings" proposed by the Forest Service instead promotes a Forest-wide homogenization of habitat via deer edge effects.

Conclusions

Our understanding of edge effects is still in its infancy. Edge effects on the scale of several km resemble those already suggested for other forests (Janzen 1983, 1986), but remain politically controversial due to their management implications. Studies are now under way that should eventually allow us to tailor the size and shape of reserves specifically to retain a full complement of plant and animal species. Such areas, if they prove unnecessarily large, can always be reduced in size at a later time, but cannot be expanded without losing decades of forest growth.

Maintaining the proposed 200 to 400 km^2 reserves of contiguous habitat within the National Forests to retain species sensitive to deer browsing or otherwise dependent on forest interior habitats would be simple and inexpensive (Task Force 1986). Such areas would also be freely available for a wide variety of other uses, including hunting (intensified for deer, if possible), fishing, snowmobiling, skiing, hiking, camping, and small-scale wood removal. They would, however, exclude commercial-scale timber harvests, "wildlife openings," and new road construction, all of which create large amounts of edge habitat. Such management would probably not reduce the total deer populations of the area, but would alter the spatial distribution of deer, allowing local reductions in deer abundance and consequent survival of sensitive species. Encouragingly, the staff of the Chequamegon National Forest concluded that such areas could be created without losing jobs or sacrificing timber production or other outputs of their Forest (J. Wolter, personal communication 1986). Disappointingly, the regional office of the U.S. Forest Service, perhaps concerned about the precedent such areas would establish, reversed this decision without any formal scientific or economic review. Currently these issues are being considered by the chief of the U.S. Forest Service.

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