PREDICTORS OF WHITE-TAILED DEER GRAZING INTENSITY IN FRAGMENTED DECIDUOUS FORESTS

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Abstract: White-tailed deer (*Odocoileus virginianus*) can cause major changes in the composition and structure of forest communities by browsing shrubs and tree seedlings and grazing understory forbs. Such effects have become an increasingly pervasive management concern in protected natural areas and parks where conservation of native plant communities is a primary objective. The magnitude of these effects can vary widely according to variations in local deer numbers and availability of alternate food sources. We used measurements from 11 maple–basswood forest fragments in southcentral Minnesota to examine the predictability of deer grazing intensity on understory forbs based on local winter deer density, composition of the landscape surrounding each forest fragment, and characteristics of forb populations within the forest. In early summer, grazing intensity on 6 palatable forb species at most sites was inversely correlated with the availability of alfalfa within a 1.5-km radius of the stand ($r^2 = 0.66$); winter deer density and forb flowering rate within the stand were additional important predictors of grazing intensity. Later in the growing season, most variability in the intensity of grazing among forest fragments could be explained either by the availability of row crops, alfalfa, and fields within a 1.5-km radius of the stand ($r^2 = 0.75$) or by a combination of winter deer density and forb abundance within the stand ($r^2 = 0.75$). Results show that parks and preserves with low densities of palatable plant species in the forest understory may be especially susceptible to effects of deer grazing. Changes in landscape composition (e.g., increased row-cropping or conversion of land to residential developments) should be an important consideration in the management of deer densities in areas designed to protect native forest communities.

Over the past 150 years, much of the deciduous forest region of the upper midwestern United States (Minnesota, Wisconsin, Michigan) has been converted to agriculture (Stearns 1988). Only approximately 2% of old-growth hardwood forests remain, with mostly small, scattered woodlots in the southern regions of these states (Frelich 1995). During the 1800s, white-tailed deer were extirpated in many areas, but populations recovered in the mid-1900s after the establishment of protective hunting laws (Gladfelter 1984). Today, deer populations often reach high densities in parks and preserves designed to protect remaining fragments of deciduous forest, with significant consequences for these plant communities (Alverson et al. 1988, Miller et al. 1992, Anderson and Katz 1993, Anderson 1994).

In southcentral Minnesota, some 8,000 km² of contiguous deciduous forest dominated by sugar maple (*Acer saccharum*), basswood (*Tilia americana*), and elms (*Ulmus* spp.; Daubenmire 1936, Grimm 1984) were converted primarily to agricultural and residential land uses following European settlement. Only a few old-growth fragments remain, and most are <35 ha (Jakes 1980, Vasilevsky and Hackett 1980). The conservation of these remnants is a primary objective of the Minnesota Department of Natural Resources' Scientific and Natural Areas Program and private conservation organizations. Although deer in agricultural landscapes forage primarily on crops, they also consume understory forest vegetation in addition to using forest fragments for cover, parturition sites, and travel corridors (Nixon et al. 1991). Deer forage selectively on understory forbs in forest fragments during the summer and can have major effects on species characteristic of these forests such as trillium (*Trillium* spp.) in early summer (Augustine and Frelich 1998), and wood nettle (*Laportea canadensis*) and enchanter's nightshade (*Circaea lutetiana*) in mid–late summer (Augustine 1997).

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Effects of deer are hypothesized to be affected by deer density, landscape composition, and characteristics of the understory plant community. Managers typically use estimates of winter deer density in deciding whether and how often to control local deer densities. Whether winter deer density provides a useful indicator of summer grazing intensity within a given forest fragment is unknown, because deer migration and dispersal can result in significant seasonal shifts in density (Nixon et al. 1991). In addition, the availability of agricultural crops in the landscape surrounding forest fragments, and the abundance of understory forbs, may affect the amount of foraging by deer within a forest fragment. Finally, because deer selectively graze large flowering plants (Augustine and Frelich 1998), the availability of large plants in a population could affect the overall proportion grazed. We therefore examined the predictability of summer deer grazing intensity within maple–basswood forest fragments based on (1) local winter deer density, (2) composition of the landscape surrounding the forest fragment, and (3) characteristics of forb populations within the forest fragment.

STUDY AREA

We conducted surveys of understory vegetation at 11 old-growth, maple–basswood stands in Rice County (44°15′N, 93°20′W), Hennepin County (45°N, 93°30′W), and Wright County (45°10′N, 93°50′W) in southcentral Minnesota. Most sites were protected as Scientific and Natural Areas, state parks, or county parks, and 2 sites were privately owned. No 2 sites were <5 km apart, and all sites were considered independent of each other with regard to plant growth and deer herbivory during the growing season. The 11 stands were 5–32 ha in size, which is representative of the remaining old-growth fragments in southcentral Minnesota. All sites contained a closed canopy dominated by sugar maple, American basswood, and elms (>50% of relative dominance by basal area), exhibited an all-aged distribution of tree sizes, and contained large (50–100 cm dbh) individuals of the 3 dominant tree species (Augustine 1997). Ironwood (*Ostrya virginiana*) was an important subcanopy species. The history of these sites since European settlement was not always known, but 2 sites experienced some historic grazing by cattle and oxen. Most other sites have not been grazed by domestic livestock.

Soils were either loamy and developed from glacial deposits, or silty and developed from loess-covered glacial till (Grimm 1984). Climate is continental, cold–temperate humid, with warm summers and cold winters.

The landscape surrounding each forest fragment was a mosaic of agricultural crops, pastures and old fields, wetlands, second-growth forests, and residential developments. The predominant agricultural crops were corn, soybeans, and alfalfa.

Deer occurred at all sites but varied in density as a result of management. Deer were not hunted at 2 sites, and these had the highest densities; at other sites, deer were hunted either on a yearly or variable-year basis. Hunting is the major factor regulating deer densities. In areas with no hunting, vehicle collisions, emigration, and some poaching may be important mortality factors because no evidence of malnutrition was observed during 1994–96. Given the widespread availability of agricultural crops, high fawn pregnancy rate, and high proportion of adult does bearing twins (Harder 1980), we believe deer densities at all sites were well below ecological carrying capacity (sensu McCullough 1979). The highest deer densities occurred in winter, when deer use forest fragments for cover; deer disperse into the surrounding agricultural lands during the growing season.

METHODS
Deer Density

To examine the relation between winter deer abundance and summer grazing intensity, we used pellet-group counts to estimate winter deer density at all 11 study sites, and we used aerial counts at 6 study sites to check the pellet-count estimates. We conducted pellet counts immediately following snowmelt during 1–12 April 1996, in 45–50 50.3-m² circular plots at each site. We converted pellet counts to density of overwintering deer (deer/km²) based on a 150-day deposition period and 13 pellet groups·deer^{-1}·day^{-1} (Eberhardt and van Etten 1956). In addition, aerial counts were conducted in January 1996 by 2 deer managers from Hennepin County Parks and the Minnesota Department of Natural Resources who have counted these sites for ≥5 years. Counts were conducted when snow cover and weather were judged by the managers to maximize accuracy. A fixed-wing Piper Supercub aircraft was used

Table 1. Forb species sampled in early and late summer at 11 study sites in southcentral Minnesota, 1996.

Season	Palatability	Scientific name	Common name
Early summer	Palatable	*Trillium* spp.[a]	Trillium
	Palatable	*Uvularia grandiflora*	Large-flowered bellwort
	Palatable	*Smilacina racemosa*	False Solomon's seal
	Palatable	*Sanguinaria canadensis*	Bloodroot
	Palatable	*Smilax ecirrata*[b]	Carrion flower
	Palatable	*Polygonatum biflorum*	True Solomon's seal
	Unpalatable	*Arisaema triphyllum*	Jack-in-the-pulpit
Late summer	Palatable	*Laportea canadensis*	Wood nettle
	Palatable	*Circaea lutetiana*	Enchanter's nightshade
	Palatable	*Solidago flexicaulis*	Zig-zag goldenrod
	Palatable	*Impatiens pallida*	Jewelweed
	Palatable	*Caulophyllum thalictroides*	Blue cohosh
	Unpalatable	*Eupatorium rugosum*	White snakeroot
	Unpalatable	*Hackelia virginiana*	Stickseed

[a] *T. grandiflorum, T. cernuum, T. flexipes.*
[b] May include *Smilax herbaceae.*

at 4 sites and a Robinson R-22 helicopter at 2 sites. For each site, the area flown included the old-growth fragment sampled for understory forbs and a surrounding mosaic of second-growth forest, shrubland, and wetlands. Deer density was calculated from the number of deer observed, uncorrected for visibility, within the area flown that was also within a 3-km radius of the center of the study stand. Reported densities are the number of deer observed divided by the area of winter cover, where winter cover was defined as deciduous and coniferous forest, shrubland, and wooded wetlands.

Understory Forbs

We used systematic plot sampling to survey the abundance and proportion grazed of 7 early-summer forb species during 10–20 June and 7 late-summer forb species during 3–14 August 1996 (Table 1). Species were chosen because they are characteristic of late-successional, mesic deciduous forests (Curtis 1959, Rogers 1981). The 7 early-summer species represent a guild of long-lived, nonclonal forbs that initiate growth in spring, have a single, central stem, and flower in early June. These species were of interest because their growth form may be especially sensitive to deer, as a single bite removes most or all leaves, and no leaf regrowth occurs after being grazed.

The 7 late-summer species (Table 1) all have a single, central stem, except stickseed (*Hackelia virginiana*), which has a basal rosette of leaves and a central stem. These species flower in mid-August, except for blue cohosh (*Caulophyllum thalictroides*), which flowers in early

summer but remains green and develops fruits in late summer. Life-history strategies of the late-summer species vary widely from an annual, jewelweed (*Impatiens pallida*), to the predominantly clonally reproducing zig-zag goldenrod (*Solidago flexicaulis*).

At each site, we counted forbs in 46–50 6-m² circular plots, using 50-m spacing at 8 sites and 25-m spacing at the 3 smallest sites. For species with low abundance at a given site, we conducted additional sampling with shorter spacing between plots (80–96 6-m² plots for moderately abundant species and 145–250 6-m² plots for sparse species). In each plot, we counted the number of grazed, ungrazed, and flowering plants, where a "plant" was defined as any stem with no aboveground connection to other stems. Due to our focus on deer effects to the plants, we only counted stems as grazed if >50% of the leaf area was removed.

In the August sampling season, we distinguished between recently grazed and old-grazed stems. The definition of a recently grazed stem was based on the degree of senescence of the bite point. We developed definitions for each species based on observations of marked plants with simulated grazing that were monitored repeatedly in 1995 and 1996 such that recently grazed stems approximate a 30-day grazing rate. Late-summer grazing calculations were based on recently grazed stems only.

We defined grazing intensity as the proportion of stems of a species or group of species grazed by deer. For each site, we used Cochran's (1977:175–176) jacknife technique to calculate the proportion grazed. This method ac-

Table 2. Land-use categories used to describe composition of the landscape surrounding maple–basswood forest fragments in southcentral Minnesota, 1996.

Land-use category	Definitions
Row crops	Corn and soybean fields
Alfalfa fields	Alfalfa or alfalfa–clover–hay mixtures dominated by alfalfa or clover
Fields	Hay, old fields, pastures, restored prairie, golf courses
Deciduous forest	Contiguous canopy cover of deciduous tree species
Coniferous forest	Contiguous canopy cover of coniferous tree species
Shrubland	Noncontiguous tree canopy with >10% cover of woody species
Wooded wetlands	Wetlands with >10% cover of woody species
Nonwooded wetlands	Primarily cattail (*Typhus* spp.) and phragmites (*Phragmites australis*) marshes; wet meadows
Residential	Residential housing developments and farmsteads
Forested residential	Dispersed residences in contiguous forest cover
Urban	Industrial parks, town centers, highways, gravel pits
Open water	

counts for stems within a given plot not being independent of each other by treating the plot rather than individual stems as the sampling unit. We calculated the combined grazing intensities on all 6 palatable early-summer species and all 5 palatable late-summer species because the abundance of some individual species varied widely among sites. We also individually examined grazing intensity for the most highly palatable species in each season.

For the group of 6 palatable, early-summer forbs, we used the proportion of plants flowering as an index of the proportion of the population consisting of large individuals because flowering plants are typically the largest individuals in the population (Kawano et al. 1986, Hanzawa and Kalisz 1993). This proportion was also calculated via Cochran's (1977) jacknife technique. For late-summer species, percent flowering could not be used as an index of population size structure, because these species vary widely in life-history strategy.

Landscape Composition Surrounding Forest Fragments

To examine whether the landscape surrounding remnant forest fragments affects deer grazing intensity within a stand, we mapped composition of the landscape within a 3-km radius of each study site during ground surveys conducted from 25 May to 5 June 1996. During ground surveys, we used color infrared aerial photographs taken in April 1991 and 1992 as a base template. We digitized maps derived from the ground surveys with a Geographic Information System (GIS; ARC/INFO 3.4.2b), and we classified land use into 12 categories (Table 2).

To examine effects of availability of alternative forage sources such as row crops (soybeans, corn) and forage crops (alfalfa, clover) in the landscape immediately surrounding forest fragments on spring and summer deer grazing intensity within the stand, we calculated the proportion of total land area within a 1.5-km radius of each study site that was occupied by these agricultural crops. This distance was chosen because, during the growing season, deer in agricultural regions typically make only local movements of about 500–750 m between bedding sites and crop fields (Nixon et al. 1991).

Statistical Analysis

We examined the relation between summer deer grazing intensity and (1) winter deer density, (2) forb availability within the stand, (3) forb flowering rate, and (4) availability of alternative forage patches in the surrounding landscape via multiple linear regression (Weisberg 1985). In each analysis, we fitted regression models for all possible combinations of predictors. Comparison of the significance of overall regression F-tests, coefficients of variation, and t-statistics for significance of individual predictors were used in model selection. For early and late-summer analyses, we tested for the need to transform the response following the Box-Cox procedure for each predictor (Box and Cox 1964). This analysis indicated a nonlinear relation between grazing intensity on late-summer forbs and all 3 predictors, and between grazing intensity on wood nettle and all 3 predictors. The analysis conducted for each predictor separately suggested a 0.15–0.35 power transformation, so we used 0.25.
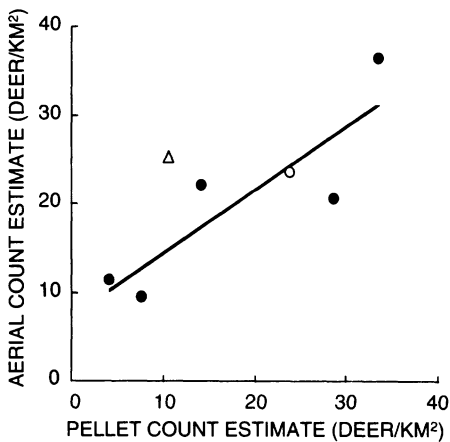
Fig. 1. Correlation between estimates of winter deer density for 6 maple–basswood forest fragments in southcentral Minnesota, based on pellet counts versus aerial counts. Solid circles show results for 5 study sites for the 1995–96 winter. Open symbols show density estimates for a sixth site where the pellet count estimate changed significantly between 1994–95 (triangle) and 1995–96 (circle), but the aerial count was nearly identical in both years. From the 1994–95 data for this latter site: [(aerial deer/km²) = 1.064 (pellet deer/km²) −3.270; $r^2 = 0.76$, $P = 0.024$].

RESULTS

Deer Density

Winter deer densities based on pellet counts varied between 0.7 and 33.4 deer/km² among study sites. Inspection of the relation between aerial count estimates and pellet count estimates at sites where both were conducted ($n = 6$) identified 1 site where results were inconsistent (Fig. 1). At this site, pellets probably underestimated density due to a local shift in habitat use to adjacent south-facing shrubland and 2 nearby conifer stands during the more severe winter of 1995–96, which included low mean temperature, high snow depths, and a long period of snow cover. We also surveyed this site with both methods during the more mild winter of 1994–95. Aerial counts indicated the same density between years, while pellet counts were dramatically lower in 1995–96 compared to 1994–95 (Fig. 1). In subsequent analyses, the 1995 pellet estimate was used for the site where the 1996 result was a known underestimate. A strong linear relation was observed between pellet count and aerial count estimates: [aerial deer/km² = 1.064 (pellet deer/km²) − 3.270]; ($F_{1,4} = 12.68$, $r^2 = 0.76$, $P = 0.024$; Fig. 1). Analysis of the landscape within a 3-km radius of the 5 study sites where aerial counts were not conducted indicated pellet counts were not

likely to have underestimated local deer density, because alternative winter habitat was absent.

Grazing Patterns

Surveys documented selective foraging on understory species. Grazing in early summer was focused on species in 6 genera (*Sanguinaria, Smilacina, Smilax, Polygonatum, Trillium, Uvularia*; Table 1), while jack-in-the-pulpit (*Arisaema triphyllum*) was consistently avoided. Stems of early-summer species grazed in the first week of spring may have senesced prior to sampling in June, but no other grazed stems are believed to have been missed. The range of grazing intensities observed among sites was 1.0–37.0% for the most palatable species (trillium), 1.2–9.6% for all 6 palatable species combined, and 0.0–4.1% for jack-in-the-pulpit. In late summer, species in 5 genera experienced high grazing intensity (*Laportea, Circaea, Impatiens, Solidago, Caulophyllum*; 0.4–35.5% for all 5 combined), with the highest grazing intensity on wood nettle (0.2–72.4%). Two other species, white snakeroot (*Eupatorium rugosum*) and stickseed, were avoided by deer (0.0% grazed) in late summer at the sites where these species occurred.

Predictors of Grazing Intensity

Regression models showed no evidence of nonconstant variance, nonlinearity, or nonnormality based on the diagnostics outlined by Weisberg (1985:128–163), although the small sample size limited the power of tests for nonnormality.

Early Summer.—Regression analyses showed that alfalfa availability alone was the most important predictor of grazing intensity ($F_{1,9} = 5.14$, $P = 0.049$) but explained only a third of the variability among sites. Grazing intensity was inversely related to alfalfa availability ($r^2 = 0.36$), with 1 clear outlier (Fig. 2). When this site was excluded, alfalfa availability explained most variation among sites in grazing intensity ($F_{1,8} = 15.20$, $r^2 = 0.66$, $P = 0.005$; Fig. 2).

The outlier site was unusual in the low abundance (0.09 stems/m²) and low flowering rate (1.9%) of palatable, early-summer forbs. Flowering rates of long-lived, early-summer forbs may be low due to effects of historic grazing by domestic livestock, historic grazing by deer at sites with high deer density, or both. The counteracting influences of high deer density but few large, flowering plants could result in an
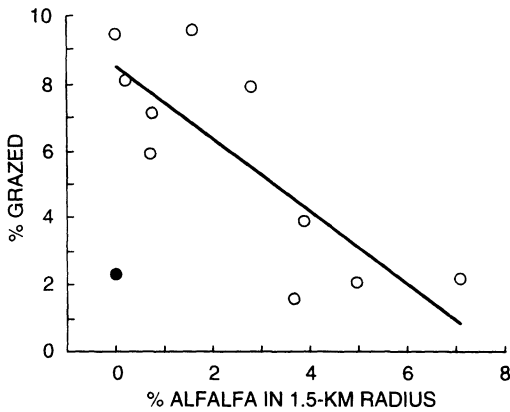
Fig. 2. Correlation between availability of alfalfa (percentage of the landscape within a 1.5-km radius of each stand occupied by alfalfa fields) surrounding 11 forest fragments in southcentral Minnesota and deer grazing intensity on 6 palatable, early-summer forb species in 1996. The solid circle shows 1 outlier site. Exclusive of this site, a highly significant inverse relation was observed ($r^2 = 0.66$, $P = 0.005$).
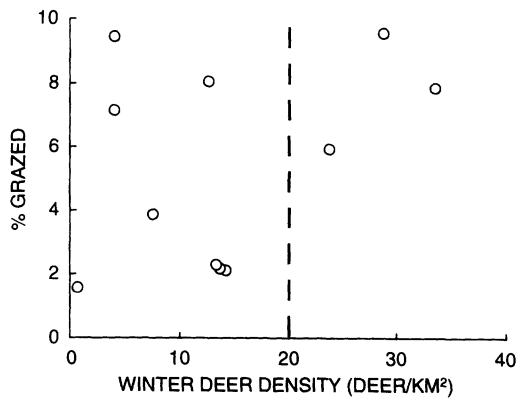

Fig. 3. The relation between winter deer density based on pellet group counts at each of 11 forest fragments in south-central Minnesota and grazing intensity on 6 palatable, early-summer forb species in 1996. The dashed line separates sites with high deer density and high grazing intensity from sites with low deer density and variable grazing intensities.

intermediate level of grazing on the overall population in a given forest fragment. Because such interactions may be difficult to detect with the small number of sites in this study and the scatterplot for winter deer density versus grazing intensity (Fig. 3) showed a pattern that cannot be directly analyzed with standard regression techniques (Thomson et al. 1996), we examined this interaction with categorical rankings for deer density (high vs. low) and flowering rate (high vs. low). Based on figure 3, sites were given a deer density rank of 1 if winter deer density was >20/km², and zero for lower overwinter density. Similarly, the 2 sites with the lowest flowering rate for palatable, early-summer species were assigned a categorical flowering rate rank of zero, with all other sites equal to 1. When these 2 variables were included in a multiple regression with alfalfa availability, all 3 were significant predictors of grazing intensity: [percent grazed = 2.72 − 1.07 (alfalfa) + 3.39 (deer density rank) + 5.27 (flowering rank)]; ($F_{3,7} = 15.70$, $r^2 = 0.87$, $P = 0.002$; alfalfa: $t = 5.08$, $P = 0.001$; deer rank: $t = 3.62$, $P = 0.009$; flowering rank: $t = 4.41$, $P = 0.003$).

Among the 6 early-summer, palatable forbs, trillium was consistently the most preferred. For all sites where trillium occurred ($n = 10$), a regression analysis examining winter deer density, alfalfa availability in the surrounding landscape, trillium abundance (stems/m²), and trillium flowering rate suggested winter deer density was the most significant predictor of

grazing on trillium ($F_{1,8} = 6.79$, $r^2 = 0.46$, $P = 0.031$). Inspection of the scatterplot of percent grazed versus alfalfa availability again showed a strong inverse relation, with 1 obvious outlier (Fig. 4). When the outlier was excluded, alfalfa availability was a highly significant predictor of grazing intensity ($F_{1,7} = 13.26$, $r^2 = 0.65$, $P = 0.008$; Fig. 4). This outlier was the highest deer density site. We did not find a significant correlation between trillium abundance or flower-
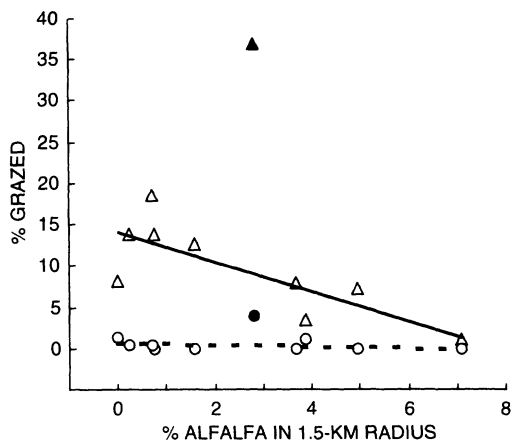

Fig. 4. Correlation between alfalfa availability (percentage of the landscape within a 1.5-km radius occupied by alfalfa fields) and the percentage of trillium (triangles) and jack-in-the-pulpit (circles) stems grazed at 11 forest fragments in southcentral Minnesota in 1996. Grazing intensity for both species was much higher than expected, based on alfalfa availability at the highest deer density site (solid symbols). For the other sites, alfalfa availability was a highly significant predictor of grazing on trillium (open triangles; $r^2 = 0.65$, $P = 0.008$), while grazing on jack-in-the-pulpit was consistently close to zero and unrelated to alfalfa availability (open circles; $P = 0.51$).
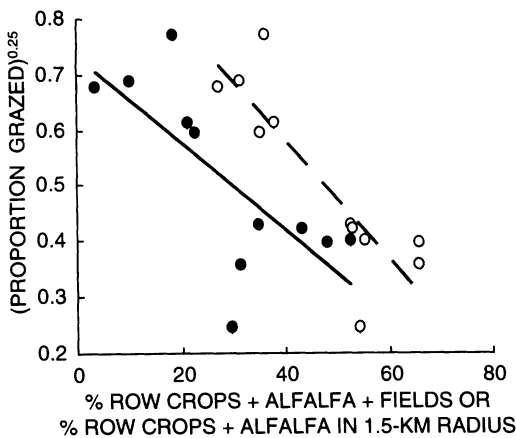
Fig. 5. Correlation between alternative forage availability in the vicinity of each of 11 forest fragments in southcentral Minnesota and deer grazing intensity on 5 late-summer palatable forb species in 1996. Results are for 2 closely related measures of alternative forage: percent row crops, alfalfa, and fields within a 1.5-km radius of the stand (open circles, dashed line: $r^2 = 0.75$, $P = 0.001$), and percent row crops and alfalfa within a 1.5-km radius of the stand (closed circles, solid line: $r^2 = 0.53$, $P = 0.011$).
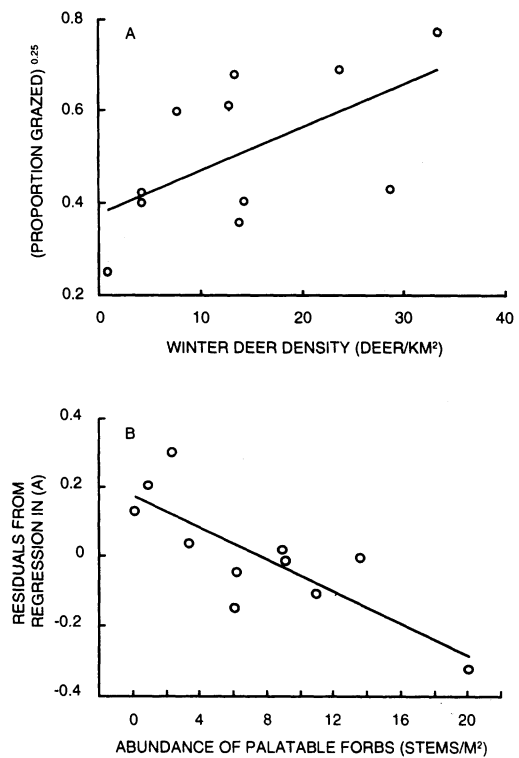

Fig. 6. (A) Correlation between winter deer density at 11 forest fragments in southcentral Minnesota and deer grazing intensity on 5 late-summer forb species in 1996, and (B) the residuals from (A) as a function of palatable forb abundance (stems/m²) within each stand ($r^2 = 0.75$; winter deer density: $P = 0.009$; forb abundance: $P = 0.007$).

ing rate within a stand and grazing intensity ($F_{1,8} \leq 2.65$, $P \geq 0.142$).

The degree of selective foraging by deer in early summer was exemplified by the contrast between the high observed grazing intensities for trillium at certain study sites and the consistent avoidance of a morphologically and phenologically similar forb, jack-in-the-pulpit (Fig. 4). Grazing intensity on this latter species was consistently near zero at all sites (Fig. 4).

Late Summer.—For palatable, late-summer forbs, most variation in deer grazing intensity among sites was explained by the combination of winter deer density, abundance of palatable forbs within each stand, and percentage of the surrounding landscape consisting of alfalfa, row crops, and fields ($F_{3,7} = 22.01$, $r^2 = 0.90$, $P = 0.001$). Highly significant predictors were deer density ($t = 3.15$, $P = 0.016$) and the combined availability of alfalfa, row crops, and fields ($t = 3.34$, $P = 0.012$), while forb abundance was marginally significant ($t = 2.20$, $P = 0.064$). A combination of winter deer density and palatable forb abundance within the stand accounts for much of the variability in grazing intensity ($F_{2,8} = 12.13$, $r^2 = 0.75$, $P = 0.004$; deer density: $t = 3.44$, $P = 0.009$; forb abundance: $t = 3.61$, $P = 0.007$). However, an equally valid explanation for a similar level of variation is provided by the availability of row crops, alfalfa, and fields as the only predictor ($F_{1,9} = 26.40$, r^2

$= 0.75$, $P = 0.001$) or, to a lesser degree, just by the availability of row crops and alfalfa ($F_{1,9} = 10.08$, $r^2 = 0.53$, $P = 0.011$; Figs. 5, 6).

Analyses for the most intensively grazed late-summer species, wood nettle, showed the same patterns as with all palatable, late-summer species combined. A multiple linear regression with winter deer density, wood nettle abundance, and availability of row crops, alfalfa, and fields in the surrounding landscape showed all 3 are significant predictors of grazing on wood nettle ($F_{3,7} = 21.41$, $r^2 = 0.90$, $P = 0.001$; deer density: $t = 3.31$, $P = 0.013$; wood nettle abundance: $t = 2.60$, $P = 0.036$; row crops, alfalfa, and fields: $t = 2.87$, $P = 0.024$). As with all late-summer palatable species, most of the variation in grazing on wood nettle could be explained either by the combination of winter deer density and nettle abundance ($F_{2,8} = 14.7$, $r^2 = 0.79$, $P = 0.002$) or the availability of row crops, alfalfa, and fields ($F_{1,9} = 21.89$, $r^2 = 0.71$, $P = 0.001$).

DISCUSSION

Understanding how management can influence the effects of large mammalian herbivores on plant communities is critical for the successful conservation of small fragments of native plant communities. Where native forests have been largely replaced by intensive agriculture, many conservation efforts are focused on protecting remaining forest fragments, but high levels of white-tailed deer herbivory can dramatically alter components of the native community (Alverson et al. 1988, Anderson and Katz 1993, Anderson 1994, Waller and Alverson 1997, Augustine and Frelich 1998).

Our results indicate that for managers to successfully mitigate deer effects on fragmented native plant communities, goals for acceptable numbers of deer in a given park or preserve must be considered in the context of the local landscape and the condition of populations of sensitive plant species. In particular, the seasonal availability of agricultural crops is a critical factor influencing grazing intensity within forest fragments. In early summer, fields of row crops are still bare soil, and residential developments provide limited forage resources compared to the high-protein forage in alfalfa fields. The inverse correlation between alfalfa availability and grazing pressure on all 6 palatable, early-summer forbs and on trillium alone indicates seasonal availability of different crops can strongly influence deer effects on forbs of small forest reserves.

Simultaneously, the level of grazing intensity within forest fragments is not fully explained by landscape composition: deer density is clearly an important factor. Low grazing intensity was never observed where winter deer densities were >20 deer/km^2 (Fig. 3). Thus, increased alfalfa availability may not dramatically reduce grazing in areas with high deer density. Conversely, differences in grazing intensity among sites with lower deer densities (Fig. 3) were mainly negatively associated with alfalfa availability. Therefore, management to reduce deer densities may not reduce grazing on sensitive forest forbs unless alternative forage sources are available in the surrounding landscape. Where alternative forage is not available and cannot be provided through management (e.g., urban parks), extremely low densities or no deer (e.g., deer-proof fencing or deer removal) may be

necessary to conserve the most highly palatable species.

The lower grazing intensity on early-summer forbs observed in forest fragments with low flowering rates of forbs likely reflects that such populations consist mainly of small plants. Because deer in farmlands appear to use forests mainly for cover, travel, and fawning (Nixon et al. 1991), and show highly selective foraging (Fig. 4), they bypass small nonflowering plants. Nevertheless, a forb population with low flowering rate would still be adversely affected due to deer selectively grazing on the few reproducing individuals. Thus, although information on size structure in forb populations may not be necessary to gauge immediate effects of deer, this factor should be considered by managers conducting understory surveys to assess grazing intensity.

For late-summer forbs, we identified 2 potential explanations for the wide variation in grazing intensity among sites. First, by midsummer, row crops provide highly palatable forage for deer, and fields (primarily old fields, hay fields, golf courses) provide an additional forage source. Availability of row crops and alfalfa was correlated with late-summer grazing intensity, and a significant additional amount of variation in grazing was related to availability of fields (Fig. 5). This correlation again suggests the critical role of adjacent crops relative to floral conservation in small parks and preserves.

Alternatively, much of the variation in late-summer grazing among study sites was also associated with winter deer density and forb abundance. Forb abundance in late summer, which varied among sites from 0.01 to 20 stems/ m^2, showed a clear, negative linear relation with the transformed grazing values, after controlling for local deer density (Fig. 6). Grazing intensity was much higher than expected from deer density alone at sites where forb density was extremely low, decreased rapidly with increasing forb abundance, and remained at a consistently lower level than expected, based on deer density, where palatable forbs are abundant. Above a threshold of forb abundance, deer may simply not forage enough inside forest fragments to remove most of the available stems, but a similar level of forb consumption removes most stems when they are rare.

Distinguishing between the relative importance of landscape composition versus winter deer density plus forb abundance is difficult be-

cause they are in part collinear. Sites with more residential neighborhoods in the landscape, and therefore fewer agricultural fields, also have limited hunting opportunities, and hence high deer densities. However, our regression analysis showed that after accounting for variability in grazing associated with landscape composition, both deer density and forb abundance were important predictors of grazing intensity. Comparison of deer grazing pressure on wood nettle at 2 forest fragments with a similar landscape (18% vs. 10% alfalfa and row crops; 18 vs. 21% fields) and high deer density (>20 deer/km^2) illustrates the important influence of forb abundance on deer grazing pressure, in addition to landscape composition. Where wood nettle was rare (0.01 stems/m^2), deer consumed most available stems (72%), and no flowering plants were observed. However, at the site where this species was abundant (3.7 stems/m^2), deer were only able to consume 25% of stems, and 27% were flowering in mid-August (Augustine 1997).

MANAGEMENT IMPLICATIONS

Deer density has often been identified as the critical factor determining the degree to which deer affect plant communities (Alverson et al. 1988, Anderson 1994). For protected forest remnants in southcentral Minnesota, local deer numbers are either controlled through some format of public hunting or there is no managed control. Where herd control is directed toward protecting native vegetation, decisions on hunts are based mainly on winter deer density, with little or no information concerning threats to herbaceous plants due to summer grazing of deer. Our results show that winter deer density does provide managers with important information concerning deer effects on forest community conservation in small forest preserves: where winter densities were >20 deer/km^2, high grazing intensity was consistently observed during the growing season.

However, this analysis shows that numbers of deer should not be the only consideration in management: landscape composition and forb abundance are also critically related to the effect deer can exert on a particular site. First, where current populations of sensitive forest forbs are unusually sparse, deer herbivory should be recognized as a serious potential threat to the local survival of such populations. Secondly, the availability of alfalfa and row crops in the surrounding landscape has seasonal

influences on deer grazing in forest fragments. Where winter deer numbers were <20/km^2, early-summer forb grazing was much lower at sites where alfalfa was available compared to sites where alfalfa was not available. Also, late-summer grazing was quite low where some combination of row crops, alfalfa, and fields surrounded the forest fragment, as well as where there was less agriculture but palatable forest forbs were extremely abundant. If the surrounding landscape is being altered with reduced cultivation of alfalfa or increased conversion of row crops to residential developments, then there may be a corresponding need to further reduce local deer numbers.

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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. 1994. Height of white-flowered trillium (*Trillium grandiflorum*) as an index of deer browsing intensity. Ecological Applications 4:104–109.

———, AND A. J. KATZ. 1993. Recovery of browse-sensitive species following release from white-tailed deer *Odocoileus virginianus* Zimmerman browsing pressure. Biological Conservation 63:203–208.

AUGUSTINE, D. J. 1997. Grazing patterns and impacts of white-tailed deer in a fragmented forest ecosystem. Thesis, University of Minnesota, St. Paul, Minnesota, USA.

———, AND L. E. FRELICH. 1998. White-tailed deer impacts on populations of an understory forb in

fragmented deciduous forests. Conservation Biology 12:in press.

BOX, G. E. P., AND D. R. COX. 1964. An analysis of transformations (with discussion). Journal of the Royal Statistical Society Series B 26:211–246.

COCHRAN, W. G. 1977. Sampling techniques. Third edition. John Wiley & Sons, New York, New York, USA.

CURTIS, J. T. 1959. The vegetation of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.

DAUBENMIRE, R. F. 1936. The "Big Woods" of Minnesota: its structure and relations to climate, fire and soils. Ecological Monographs 6:235–268.

EBERHARDT, L., AND R. C. VAN ETTEN. 1956. Evaluation of the pellet group count as a deer census method. Journal of Wildlife Management 20:70–74.

FRELICH, L. E. 1995. Old forest in the Lake States today and before European settlement. Natural Areas Journal 15:157–167.

GLADFELTER, H. L. 1984. Whitetail populations and habitats: Midwest agricultural region. Pages 427–440 *in* L. K. Halls, editor. White-tailed deer: ecology and management. Stackpole Books, Harrisburg, Pennnsylvania, USA.

GRIMM, E. 1984. Fire and other factors controlling the Big Woods vegetation of Minnesota in the mid-nineteenth century. Ecological Monographs 54:291–311.

HANZAWA, F. M., AND S. KALISZ. 1993. The relationship between age, size, and reproduction in *Trillium grandiflorum* (Liliaceae). American Journal of Botany 80:405–410.

HARDER, J. D. 1980. Reproduction of white-tailed deer in the north central United States. Pages 23–35 *in* R. L. Hine and S. Nehls, editors. White-tailed deer population management in the north central states. North Central Section, The Wildlife Society, Columbia, Missouri, USA.

JAKES, P. J. 1980. The fourth Minnesota forest inventory: area. U.S. Forest Service Resource Bulletin NC-54.

KAWANO, S., M. OHARA, AND F. H. UTECH. 1986. Life history studies on the genus *Trillium* (Liliaceae) II. Reproductive biology and survivorship of four eastern North American species. Plant Species Biology 1:47–58.

MCCULLOUGH, D. E. 1979. The George Reserve Deer Herd: population ecology of a K-selected species. University of Michigan Press, Ann Arbor, Michigan, USA.

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.

NIXON, C. M., L. P. HANSEN, P. A. BREWER, AND J. E. CHELSVIG. 1991. Ecology of white-tailed deer in an intensively farmed region of Illinois. Wildlife Monographs 118.

ROGERS, R. S. 1981. Mature mesophytic hardwood forest: community transitions, by layer, from east-central Minnesota to southeastern Michigan. Ecology 62:1634–1647.

STEARNS, F. 1988. The changing forests of the Lake States. Pages 25–35 and maps *in* W. E Shands, editor. The Lake States forests: a resources renaissance. The Conservation Foundation, Washington, D.C., USA.

THOMSON, J. D., G. WEIBLEN, B. A. THOMSON, S. ALFARO, AND P. LEGENDRE. 1996. Untangling multiple factors in spatial distributions: lilies, gophers, and rocks. Ecology 77:1698–1715.

VASILEVSKY, A., AND R. L. HACKETT. 1980. Timber resources of Minnesota's central hardwood unit, 1977. U.S. Forest Service Resource Bulletin NC-46.

WALLER, D. M., AND W. S. ALVERSON. 1997. The white-tailed deer: a keystone herbivore. Wildlife Society Bulletin 25:218–226.

WEISBERG, S. 1985. Applied linear regression. Second edition. John Wiley & Sons, New York, New York, USA.