
Use of Vegetational Characteristics and Browsing Patterns to Predict Deer Damage in Eastern White Pine (*Pinus strobus*) Plantations

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ABSTRACT: *Browsing of seedlings by white-tailed deer (Odocoileus virginianus) can make natural and artificial forest regeneration difficult. Few mathematical models predict deer browsing within and between sites, giving managers only landscape-level characteristics, such as deer population levels and yearly snowfall measurements, to determine where deer-protective measures should be installed. This study described browsing patterns and assessed influence of vegetational characteristics on browsing. Predictive models were developed using overstory and understory measurements, and browsing reconstructions of individual seedlings within eight eastern white pine (Pinus strobus) plantations in northern Minnesota. Results indicated that deer concentrate browsing on terminal leaders in shorter seedlings, shifting to laterals as seedlings approach browsing height limits (140 cm). Damage models were site-specific. The vertical and horizontal distribution of understory vegetation and the presence of alternative food sources influenced the probability of browsing. Future models should incorporate these measures as well as browse selection patterns, landscape-level characteristics, and past deer activity. North. J. Appl. For. 16(2):96-102.*

Seedling depredation by white-tailed deer (*Odocoileus virginianus*) is a serious threat to the establishment of both naturally and artificially regenerated stands of many tree species (e.g., Sauerman 1992). These regeneration failures can lead to substantial changes in forest canopy composition over time (Frelich and Lorimer 1985, Kittredge and Ashton 1995). Although measures such as fencing, budcapping, tree shelters, and chemical sprays can protect seedlings from deer, these measures add significantly to the cost of plantation establishment (Palmer et al. 1985, DeYoe and Schaap 1987). Therefore, in many forestry systems, damage prediction is of utmost concern to the land manager.

Most damage prediction models are site specific, overly complex, or not intended to serve a management function (Gill 1992). For example, Conover (1989) attempted to create a browsing damage model for several Connecticut nurseries and found that browsing intensity on Japanese yew (*Taxus* spp.) could only be correlated to pellet-group numbers and deer densities in adjacent woodlands and not to any characteristic of the nurseries themselves. Later, he could not explain region-wide patterns of nursery crop damage using a variety of winter weather, vegetational, and deer population indices (Conover and Kania 1995). Using a 17-variable model, McIntyre (1975, as cited in Gill 1992) explained between 51–87% of the variation in percentage of trees damaged by red deer (*Cervus elaphus*) bark stripping. However, his model proved much too complex for management purposes.

On the other hand, useful and simple damage models have been developed. For example, Welch et al. (1991) monitored 14 sites in western Scotland over the course of several years for red and roe deer (*Capreolus capreolus*) browsing on Sitka spruce (*Picea sitchensis*). They described a trivariate model—density of trees > 60 cm tall, percent cover of ericoid plants, and deer density as measured by pellet group counts—which

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explained 51.2% of the variation in leader browsing. They suggested that narrower tree spacings and planting ericoid shrubs for alternative forage in winter would reduce damage in Sitka spruce plantations.

Our study examined white-tailed deer browsing incidence within several eastern white pine (*Pinus strobus*) plantations in northern Minnesota. In this region, white pine is a second-level preference winter browse species, being slightly less preferred than northern white cedar (*Thuja occidentalis*) and red maple (*Acer rubrum*), and as preferred as yellow birch (*Betula alleghaniensis*) and jack pine (*Pinus banksiana*) (Blouch 1984). As a result, browsing pressure is a primary limiting factor to successful establishment of white pine in a forest (Sauerman 1992). The primary objectives of the study were to (1) describe patterns in browse selection by white-tailed deer (e.g., selection for a particular seedling height, selection for previously browsed seedlings, browse partitioning between laterals and terminals, etc.); (2) quantify growing conditions for each seedling using several vegetational characteristics and try to correlate these characteristics to browsing activity on each site; and (3) address the issue of risk assessment and the extent to which deer damage on any particular site could be predicted from vegetational characteristics of that site. We hypothesized that horizontal and vertical distribution of understory vegetation in the neighborhood of a seedling should influence browsing incidence within any given site.

Methods

Field Measurements

We selected eight white pine plantations in northern Minnesota as study sites to minimize site-to-site differences in both overstory composition and deer pressure (Table 1). These plantations all (1) occurred under overstories dominated by sugar maple (*Acer saccharum*), basswood (*Tilia americana*), northern red oak (*Quercus rubra*), paper birch (*Betula papyrifera*), or some combination of these species; (2) were less than 10 yr old and had a majority of seedlings under 1.4 m (4.5 ft) tall [the browsing height limit for white-tailed deer (Prior 1983), although deer can reach 2.1 m (7 ft) by standing on their hind legs (Beals et al. 1960)]; and (3) were not mechanically or chemically treated within the past 2 yr. All sites were budcapped during prior winters; this treatment installed a physical barrier (a 10 × 20 cm sheet of paper) that is stapled over the seedling terminal to discourage deer browsing on the terminals.

In July and August 1996, we placed 0.01 ha circular plots within each site such that the full spectrum of overstory and understory densities were sampled. We accomplished this by walking through the site and visually assessing the range of overstory basal areas and understory densities. Using a random number generator, transects were then distributed across the site to sample areas of average and extreme overstory and understory densities.

Table 1. Northern Minnesota site descriptions, sampling intensities, and browsing summaries as surveyed in July and August 1996.

Location	Dominant overstory species	Ave. basal area (m ² /ha)	Soil	Age (yr)	Size (ha)	Regional deer den. (indiv/km ²) ^a	No. of Plots	No. of seedlings	% browsed		
									Terminal	Lateral	Total
Itasca County	Red oak Sugar maple Paper birch	12.4	Loamy sand	6	10	5.7	14	117	9	20	21
Itasca County	Sugar maple Paper birch White pine	8.3	Sandy loam	5	5	5.7	9	56	7	20	20
Itasca County	Paper birch Sugar maple White pine	12.7	Sandy loam	3	3	5.7	12	99	22	67	68
Itasca County	Paper birch Sugar maple White pine	16.6	Sandy loam	6	6	5.7	8	76	4	5	9
Itasca County	Paper birch Basswood Sugar maple	18.7	Silt loam	3	10	5.3	17	51	6	16	20
Crow Wing County	Pin oak Red oak Bur oak	10.4	Sand	3	2	2.8 ^b	7	92	46	72	78
Cass County	Paper birch Aspen Red oak	21.2	Loamy sand	6	3	5.9	13	90	31	52	53
Cass County	Red oak Aspen	12.0	Loamy sand	10	3	5.9	14	107	2	19	19

^a Average deer density was calculated from 1994–1996 Department of Natural Resources population modeling data (Dexter 1996).

^b Site occurs within deer management zone with large amounts of agricultural fields and other poor quality habitat. Effective deer densities during winter are greater.

Plots were similarly placed at random locations along each transect. Sampling intensity averaged 11.8 plots per site (range: 7–17) and was greater on variable sites.

From the center of each plot, overstory species were sampled using a 1 m²/ha basal area factor prism. For each white pine seedling in the plot, total height and diameter at 5 cm above ground were measured. Browsing histories on each sampled seedling were reconstructed by noting the number and age of browsed terminals and laterals; reconstructions had yearly periodicity and corresponded to the period between budset in August to budbreak in May of the following year (i.e., 1995 refers to August 1995 to May 1996), the period when most deer damage occurs in northern Minnesota (P. Jordan, pers. comm., 1996). In most cases, reconstructions were reliable 2–3 yr back from the date of observation. Understory vegetation was characterized surrounding each seedling by percent covers, stem densities, and visual obstruction measurements (Table 2). Visual obstruction measurements were taken with a Robel pole (Robel et al. 1970) at a height of 1.5 m, 10 m from the seedling, and replicated four times, once in each quadrant surrounding the seedling. Visual obstruction measurements are correlated to the biomass of surrounding vegetation (Robel et al. 1970) and are very similar to point-intercept methods to assess vertical structure of understory vegetation (Davis 1997).

Data Analysis

Chi-square tests of homogeneity (Ott 1988) were used to determine potential influence of seedling height on browse selection. Seedlings were assigned to 10 cm height classes and classified as browsed or unbrowsed both for terminals and for laterals in 1995. In order to reduce the influence of small expected cell counts on χ^2 , classes were combined until at least 15 seedlings occurred in each height class (Cochran 1954). To quantify the relationships between seedling height and browsing incidence (% browsed), linear regressions that used the average height of seedlings within each 10 cm height class were conducted. Contingency table analysis and chi-square tests of independence were used to test whether seedlings that have been browsed have a higher probability to be browsed again, as indicated by an interaction between browsing in 1994 and

browsing in 1995. Throughout these tests, the arcsine transformation was calculated to average percentages.

The ability to use neighboring vegetation to predict browsing incidence was tested using multivariate logistic regression on plot averages (Neter et al. 1983, Hosmer and Lemeshow 1989). For this analysis, the logit transformation was used to linearize the dependent variable, and weighted least squares linear regression was used to estimate the coefficients of the logistic model:

$$P_{br} = \frac{1}{1 + e^{-(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}}$$

where P_{br} is the probability of browsing, the β 's are regression coefficients, and the x 's are the independent variables. Extreme observed plot probabilities (i.e., $p_{obs} = 0$ or 1) were modified as described in Neter et al. (1983).

For analysis of vegetational patterns, only browsing in 1995 was considered since vertical and horizontal distribution of understory vegetation can change substantially from year to year. Independent variables used in the analysis are listed in Table 2. US50 and US200, and AVVO and MIVO, were later dropped from the analysis because they were too highly correlated ($r > 0.80$ for each variable) with US100 and MEVO, respectively.

Models were selected from the remaining independent variables using the following criteria. Student's *t*-statistics were used to determine if coefficients of the variables were significantly different from zero. Variance inflation factors (VIF) were used to assess collinearity between the coefficients; models with coefficients that had VIF's greater than ten were discarded. An analysis of variance (ANOVA) *F*-ratio was used to test whole-model validity by determining if the model explained a significant portion of the variance in the data. These statistical tests were considered significant if $P \leq 0.05$. The Hosmer-Lemeshow (H-L) goodness-of-fit statistic was calculated for each model by using the "deciles of risk" grouping method (Hosmer and Lemeshow 1989). The H-L statistic tested how effective the models are in describing the original data units, in this case, the individual seedlings. Small chi-square values for this statistic indicate that the model fits the data well with no significant differences between the observed and predicted numbers of browsed seedlings.

Table 2. Names and operational definitions of variables measured in July and August 1996, and used to model browsing incidence in eight northern hardwood shelterwoods in northern Minnesota.

Variable	Definition	Unit
<i>BA</i>	Basal area of plot	m ² /ha
<i>DEN</i>	Density of nonherbaceous stems within a 0.636 m ² plot centered on the seedling	stems/m ²
<i>US50</i>	Understory cover at seedling height and within 50 cm of seedling	%
<i>US200</i>	Understory cover at seedling height and within 200 cm of seedling	%
<i>US100</i>	Understory cover at 1/2 seedling height and within 100 cm of seedling	%
<i>AVVO</i>	Average value of visual obstructions corrected for seedling height ^a	cm
<i>MIVO</i>	Minimum value of visual obstructions corrected for seedling height ^a	cm
<i>MEVO</i>	Median value of visual obstructions corrected for seedling height ^a	cm
<i>RUB</i>	Presence or absence of <i>Rubus</i> sp. within 200 cm of seedling	
<i>CORY</i>	Presence or absence of <i>Corylus</i> sp. within 200 cm of seedling	

^a Visual obstruction measures were subtracted from seedling height in order to adjust for differential deer selection relation to seedling height (Table 4).

Since an independent validation data set was not available, classification analysis was used to test model performance by assessing how often the model predicted the correct outcome with the 1995 browsing data. For the classification analysis, a 0.5 cutoff criterion was used; seedlings with $P_{br} \geq 0.5$ were classified as browsed, while those with $P_{br} < 0.5$ were classified as not browsed. The percentage of seedlings classified as browsed when actually not browsed, the percentage of seedlings classified as not browsed when actually browsed, the total percentage of seedlings misclassified, and the net percentage of seedlings misclassified were calculated. All statistical analyses were calculated using Statistix® 1.0 and Microsoft® Excel 7.0.

Results

Patterns of Browsing

On average, 38% (\bar{x}_{SITE} range = 9–78%, $n = 8$) of all seedlings within a site showed signs of browsing damage by deer within the past year (Table 1). Due in part to budcapping, damage was concentrated on laterals with only 17% (\bar{x}_{SITE} range = 2–46%, $n = 8$) of all seedlings within a site sustaining terminal leader damage within the past year (Table 1). Furthermore, deer often selected previously browsed seedlings; the hypothesis that the selection of seedlings browsed during 1995 is independent of whether or not those same seedlings were browsed during 1994 was rejected ($\chi^2 = 83.16$, 1 df, $P < 0.001$) (Table 3).

Seedling height influenced deer browsing patterns (Table 4). All seedlings having terminal leaders browsed during 1995 were less than 125 cm tall, with the most frequently browsed terminals on seedlings between 25 and 55 cm tall. Chi-square tests confirmed that browsing incidence on termi-

Table 3. Cross-classification of individual white pine seedling browsing histories for the periods of August 1995 to May 1996 and August 1994 to May 1995. Seedlings were measured in July and August 1996 under eight northern hardwood shelterwoods in northern Minnesota. Numbers in parentheses indicate the difference between observed and expected values for each cell

	Browsed in 1994	Unbrowsed in 1994
Browsed in 1995	157 (+56)	103 (-56)
Unbrowsed in 1995	109 (-56)	319 (+56)

NOTE: $\chi^2 = 83.16$, 1 df.

nals or on laterals was not independent of seedling height (terminals: $\chi^2 = 34.37$, 13 df, $P = 0.001$; laterals: $\chi^2 = 27.16$, 13 df, $P = 0.012$) (Table 4). Linear regression on 10 cm height-class averages indicated that the frequency of terminal browsing decreased significantly with seedling height ($F = 77.02$, $P < 0.001$), while lateral browsing increased significantly with seedling height ($F = 21.94$, $P = 0.001$).

Vegetational Analysis

It was difficult to create a general model that would predict browsing probability since a majority of the seedlings (62%) were not browsed in 1995, and site-to-site differences weakened most trends. Overall, six models met the three criteria of significant Student's *t*-values for the coefficients, VIFs less than ten, and a significant ANOVA *F*-ratio (Table 5).

The univariate models used MEVO, DEN, and RUB (models 1 through 3, respectively) and explained between 6.0% and 9.8% of the variation in browsing incidence within plots. However, the Hosmer-Lemeshow goodness-of-fit statistic (χ^2_{H-L}) indicated that none of the univariate models fit the data well ($P < 0.05$), and classification analysis showed that these models overpredicted the incidence of browsing by up to 19.4% (Table 5).

Table 4. Number of white pine seedlings within each 10 cm height class that were unbrowsed, had browsed terminals, had browsed laterals, or had both browsed terminals and laterals during August 1995 to May 1996. Seedlings were measured in July and August 1996 under eight northern hardwood shelterwoods in northern Minnesota.

Height class (cm)	Unbrowsed	Browsed			Total
		Terminals	Laterals	Both	
< 30	36	4	2	11	53
30–39	59	3	4	18	84
40–49	65	6	8	20	99
50–59	60	2	12	14	88
60–69	35	0	17	7	59
70–79	46	0	16	12	74
80–89	43	0	19	6	68
90–99	27	1	15	5	48
100–109	15	0	9	2	26
110–119	12	0	15	2	29
120–129	7	0	12	1	20
130–139	12	0	7	0	19
140–149	3	0	5	0	8
> 150	8	0	5	0	13
Total	428	16	146	98	688

Table 5. Logistic regression models for predicting browsing incidence on white pine seedlings under northern hardwood shelterwoods in northern Minnesota. Models were developed from eight sites measured in July and August 1996.

Model	β_n coefficients					R^2	F	χ^2_{H-L}
	β_0	MEVO	DEN	US100	RUB ^a			
1	-0.162	0.0101				0.10	11.0	39.6
2	-1.106		0.199			0.07	8.3	122.0
3	-0.603				1.161	0.06	7.0	— ^b
4	-1.035	0.0124	0.255			0.22	14.1	179.4
5	-0.626	0.0169		0.0280		0.22	14.4	13.3
6	-0.390	0.0113			1.362	0.19	11.6	10.6

^a P_{br} = probability of browsing; all other model terms as in Table 2.

^b The Homer-Lemeshow goodness-of-fit statistic cannot be calculated with models having only dichotomous independent variables (Homer and Lemeshow 1989). Therefore, this model is only appropriate for use with plot averages and cannot be applied at the individual seedling level.

Of all multivariate models, only three bivariate models met the *t*-value, VIF, and *F*-ratio criteria. All of these included MEVO, in combination with DEN, US100, and RUB (models 4 through 6, respectively; Table 5). Of the three bivariate models, the MEVO-US100 model (model 5) was most reliable. This model explained 22.3% of the variation in average browsing incidence and overpredicted this incidence by only 6.7% (Table 6). Furthermore, the H-L statistic was not significant ($P=0.10$), indicating that the model fit the data well. This model correctly predicted the incidence of browsing 64.8% of the time (Table 6). Of the remaining two bivariate models, only the MEVO-RUB model (model 6) had a nonsignificant H-L statistic ($P=0.23$; Table 5). The fit of this model was very similar to the MEVO-US100 model and explained roughly the same variation in the data (18.6%). Likewise, it overpredicted the incidence of browsing by 8.8% and correctly predicted incidence 65.0% of the time (Table 6).

Discussion

Although most seedlings with browsed terminals were shorter than 50 cm, our results indicated that seedlings of intermediate height classes (up to 130 cm) were very susceptible to terminal damage. This was consistent with the literature; for example, Welch et al. (1991) reported that most Sitka spruce seedlings having terminal leaders browsed by red deer were less than 85 cm tall and that the height classes most susceptible to leader browsing ranged from 35 to 55 cm in height. They attributed this pattern to larger terminal leader

diameters, greater prickliness, and increased secondary metabolites in the older and taller spruce seedlings. White pine, on the other hand, has much more flexible and less prickly terminal leaders than spruce of the same age; therefore, deer would be able to remove larger diameter branches at a greater height on white pine seedlings.

Lateral browsing was much more prevalent on all sites than terminal leader browsing and increased in incidence with increasing seedling height. This pattern has two possible explanations. First, there are many more laterals on a seedling than terminals; probability theory alone dictated that a seedling was more likely to have laterals browsed than a terminal leader, given that deer were not selecting for terminals as they browsed. Furthermore, browsing incidence on laterals should have increased as the number of laterals present increased with seedling height. Second, and most importantly, terminal leaders were protected with budcaps on all of the sites. Field trials with controls have shown that budcapping can prevent terminal browsing on an average 63% of seedlings on a site that would otherwise be damaged (R. Kleborn, unpubl. data). However, these trials do not account for the differential browsing pressure as it varied by seedling height and fail to recognize what seedlings may be benefited most from budcapping.

Our study, like others (e.g., Odermatt 1996), suggested that once a seedling had been browsed, it was more likely to be browsed again. Browsing events prolonged the period in which the seedling was within reach of the deer, may have reduced subsequent growth (Saunders and

Table 6. Classification analysis for logistic models presented in Table 5. Models were developed from 1996 measurements taken from eight northern hardwoods shelterwoods in northern Minnesota.

Model	Independent variables	Percent classification errors ^a			
		$C_{br}O_{nbr}$	$C_{nbr}O_{br}$	Total	Net
1	MEVO	28.3	8.9	37.2	19.4
2	DEN	25.9	11.6	37.5	14.3
3	RUB	26.5	9.4	35.9	17.1
4	MEVO, DEN	23.3	12.1	35.3	11.2
5	MEVO, US100	20.9	14.2	35.2	6.7
6	MEVO, RUB	21.9	13.1	35.0	8.8

^a Seedlings were classified as browsed (C_{br}) if the predicted probability of browsing ≥ 0.5 ; seedlings were classified as not browsed (C_{nbr}) if the predicted probability of browsing < 0.5 . O_{br} = observed browsed in 1995; O_{nbr} = observed not browsed in 1995.

Puettmann, in prep.), and increased the likelihood of the seedling being repeatedly browsed over time (Danell 1983, Danell and Huss-Danell 1985, Danell et al. 1994). Prolongment and growth reductions can allow herbivores to actively maintain "browsing lawns" of accessible vegetation. For example, Edenius (1993) suggested that moose (*Alces alces*) can adjust their foraging behavior through varying bite size to induce changes in twig biomass, morphology, and chemistry that would optimize later "food quality" of a given browse plant. Given this behavior, it is crucial that deer-protection strategies be incorporated into management of young white pine plantations. These strategies include (Rochelle 1992):

- Plant during periods in which deer populations are suppressed (i.e., after harsh winters).
- Avoid planting in or near stands with high winter deer densities, and particularly near areas of winter thermal cover.
- High planting densities of 2500–3000 trees/ha (1000–1200 trees/ac) or more will allow some seedlings to serve as "browse trees" during repeated deer visits.
- Budcapping of terminals should be done annually as soon as seedlings are strong enough to support budcaps (≈ 25 cm) and continue until seedlings are at least 100–150 cm tall.

Models that included visual obstruction (MEVO) in combination with horizontal understory cover (US100) or presence of *Rubus* sp. (RUB) were reliable predictors of browsing incidence. Even so, these models had highly variable coefficients when applied within any given site (M. Saunders, unpubl. data). Variability was not unexpected since damage models are often very site specific (Gill 1992) and heavily influenced by site factors such as overstory composition, local winter deer density, and distance to thermal cover. For example, Welch et al. (1991) reported that only 9.3% of the variation in browsing incidence could be explained by three main factors when plots were used in the analysis; this increased to 51.2% if sites were used instead. Furthermore, these models are biased if used in naturally regenerated stands since seedling and understory vegetation is much less uniformly distributed and correlated as in a plantation. Therefore, the MEVO-US100 (model 5) and MEVO-RUB (model 6) models should not be applied to raw data collected from individual seedlings, nor used for plantations outside northern Minnesota. Instead, these models should be applied to plot, or preferably site, averages and be used only as a relative index to compare browsing probabilities between sites, given similar deer populations and overstory compositions.

Regardless, both models suggested that visual obstruction and relative seedling height (in this experiment expressed together as MEVO) may be key components in assessing the probability that a seedling or plot will sustain future browsing. Together these two components expressed the vertical distribution of understory vegetation with

respect to a seedling and indicated to what extent the seedling was hidden from the herbivore. Therefore, seedlings may have had a lower probability of browsing damage when terminal leaders were shorter than the average height of understory vegetation and a higher probability when terminal leaders were above that vegetation. Other studies have found that browsing incidence increased as seedlings became isolated from other seedlings and from understory vegetation (Reimoser and Gossow 1996). However, our results suggested that the presence of understory vegetation (US100) increased the likelihood of browsing as understory cover increased. This discrepancy was likely related to both methodology and the presence of alternative food sources near the seedling. For instance, as shown in the MEVO-RUB model (model 6), the presence of *Rubus* sp. positively influenced the incidence of browsing. These plant species often grow in dense, monotypic patches and are highly preferred browse (Blouch 1984). Therefore, these species can form continuous canopies, possibly attracting deer into the area and increasing browsing incidence of underplanted white pine. To discourage the above phenomenon, managers could maintain dense and vertically diverse understories to discourage browsing without the presence of *Rubus* sp. and other preferred food sources. This understory condition is difficult to obtain and pathological concerns and growth delays due to increased understory competition might make this approach less desirable in the long run.

In conclusion, useful deer damage models are difficult to develop. Deer are unpredictable in their browsing patterns, often damaging every seedling within a plantation one year and not touching any seedling the next (Conover 1989, Conover and Kania 1995). Plot and seedling characteristics such as percent understory cover, visual obstruction, and seedling height, are useful in detecting relative trends in browsing probability, but they are weak in predicting seedling-to-seedling variation in browsing levels. Therefore, more useful models should include not only these variables, but also site- and landscape-level characteristics such as distance to thermal cover, local deer density, and yearly snowfall levels. Models might include a variety of other species in their assessment, namely alternative food sources that could attract deer to the area. For example, Augustine (1997) found that the most reliable predictor of spring and summer grazing intensity on six palatable forb species was the availability of row crops, alfalfa, and fields within a 1.5 km radius of the stand. Furthermore, given the increased probability of future browsing on one particular seedling after one browsing episode, past deer activity as measured by browsing histories might be incorporated into damage models. Lastly, models would likely have to be specific to individual plant species or groups of plant species that have the same relative palatability to the herbivore. With such a detailed model, land managers could then more effectively deal with deer pressures on their sites and concentrate their efforts on protecting sites with the greatest probability of damage.

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