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Daniel J. Harrison
Department of Wildlife
University of Maine
Orono, ME 04469
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EFFECTS OF WHITE-TAILED DEER ON POST-FIRE PLANT SUCCESSION

MIDORI SAEKI, Department of Wildlife, University of Maine, Orono, ME 04469

DANIEL J. HARRISON, Department of Wildlife, University of Maine, Orono, ME 04469

Abstract: Six deer exclosures that were constructed in Acadia National Park, Maine during 1949 - 1968 were surveyed during summer 1989. Three exclosures were located on areas burned in 1947, and 3 sites were located on unburned sites. Woody stems were tallied by 4 height classes (seedling, sapling, shrub-sized, and tree-sized classes) and ground cover was estimated within and outside exclosures. The effects of browsing on species composition and stem density were most prominent within the shrub height class (0.5 - 2.0 m); species richness and densities of heavily utilized species in the shrub height class were greater inside exclosures than in control plots. There were no significant differences in mean tree height ($P > 0.20$) or dbh ($P > 0.50$) between exclosures and adjacent controls; however, height distributions of trees differed significantly between exclosures and controls. Height distribution of vegetation was influenced by browsing to a greater extent than mean height or dbh of trees, especially for species preferred by deer. Differences in species composition, stem densities, and height distribution between exclosure and control sites were more apparent in white cedar (Thuja occidentalis) dominated habitats than in hardwood habitats. Effects of browsing on height distribution of white cedar was dependent on fire history.

Key words: Acadia National Park, browsing, exclosures, fire, Maine, Odocoileus

virginianus, succession, Thuja occidentalis, white cedar, white-tailed deer.

Exclosures are commonly used to determine the effects of grazing and browsing on plant communities (Webb et al. 1956, Stoeckler et al. 1957, Curtis and Rushmore 1958, Graham 1958, Shafer et al. 1961, Harlow and Downing 1970, Ross et al. 1970, Marquis 1981, Marquis and Brenneman 1981, Brand and Goetz 1986, Hanley 1987, Trumbull et al. 1989, Stewart and Burrows 1989). Exclosures with adjacent control sites have been used to monitor effects of browsing (Strauss 1988), to assess the influence of herbivory on long-term plant succession (Ross et al. 1970, Whitney 1984), and to study the effects of herbivores on short-term plant regeneration (Shafer et al. 1961, Trumbull et al. 1989).

Despite the utility of exclosures in quantifying effects of herbivory, inherent limitations should be recognized. First, the vegetation within exclosures may be affected by herbivory prior to exclusion. Therefore, the original vegetative composition, density, and genetic profile of an exclosure are the result of herbivory through evolutionary time (Edwards and Gillman 1987). Second, physical and physiological effects of browsing cannot be separated from herbivore selectivity (Strauss 1988) unless all characteristics of the vegetation (species composition, genetic variability, dispersion, and size) were originally identical in exclosures and control sites. Therefore, conclusions apply to recent influences of herbivores, and assume that the presence of herbivory is the only factor contributing to vegetational differences between exclosures and controls.

Exclosure methodology is particularly well suited for assessing the short-term (0 - 100 year) effects of herbivores on successional changes in the structure and composition of plant communities following disturbance. This study used exclosures erected 2 to 4 years after a large (6,956 ha) fire (Bar Harbor fire of 1947) to assess the influence of

browsing by an unharvested deer population on post-fire succession in Acadia National Park (ANP), Mount Desert Island (MDI), Maine. Additionally, 2 exclosures were surveyed on an adjacent large (2,660 ha) island (Isle au Haut, ANP) that maintains similar late-successional vegetation as MDI, has not burned during the past 100 years, and has maintained high densities of deer (Klatske 1968) for > 50 years. Specific objectives were to compare species composition and density of plants, by height class, between exclosures and control sites; and to compare the effects of deer browsing among areas with different vegetation types and fire histories.

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Study Area

Acadia National Park includes 17,100 ha of land and fresh water on Mount Desert Island (MDI), Isle au Haut (IH), and Schoodic Peninsula, Maine. Vegetation of ANP is categorized as spruce-fir-northern hardwood forests (Westveld et al. 1956), dominated by red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), gray birch (*B. populifolia*), and red maple (*Acer rubrum*), with understories of alder (*Alnus* spp.), highbush blueberry (*Vaccinium* spp.), and lambkill (*Kalmia angustifolia*).

The Bar Harbor fire of 1947 burned 6,956 ha of the northeast section of MDI, including 4,117 ha in ANP (F. H. Arnold, W. L. Sanage, and R. B. Moore. Natl. Park Serv. Reg. 1, Unpubl. Rep. 1948). Regenerating deciduous trees, primarily aspens (*Populus* spp.) and

birches (*Betula* spp.), replaced coniferous forests on most of the burned area. These species were heavily utilized by deer (Saeki 1991), and the increased browse availability associated with the fire resulted in increased deer populations from 400-500 in 1948 to approximately 3,000 deer in the late 1950's (R. L. Shaw, Natl. Park Serv. Unpubl. Rep., Acadia Natl. Park, 1985). Although hunting had been prohibited in ANP since 1905, over 800 deer were removed from MDI during 1960-67 as part of a herd reduction program in response to perceived over-browsing (McLaughlin 1968). Deer populations on MDI gradually declined during the 1960's (S.D. Schemnitz and M.W. Coulter, unpubl. data, 1968). McLaughlin (1968) concluded that overall browsing intensity on MDI had declined to levels compatible with production by the late 1960's, whereas Allen (1970) concluded that localized over-browsing continued to occur on historical wintering areas. Gilbert and Harrison (1982a) concluded that widespread over-browsing was not occurring on MDI in 1980, whereas Saeki (1991) concluded that overall browse utilization declined and deer became more selective foragers on MDI from 1980 to 1989.

In contrast to MDI, Isle au Haut (IH) has not burned during the past 100 years. Deer populations have been high there for at least several decades, and Baird (1966) reported overbrowsing at an estimated population density of 9.9 deer/km² in 1965. Saeki (1991) concluded that browsing intensity by deer was lower on IH than on MDI in 1989.

METHODS

Four exclosures on MDI were constructed 2-4 years following the 1947 fire, including 3 exclosures on burned areas. Additionally, 2 exclosures were constructed on IH in 1967-68. These sites ranged in size from 10 x 10 m to 15 x 15 m. Exclosures were constructed of wooden poles and 2.5 m tall wire fence with 10 x 10 cm mesh. Two control plots were established <75 m from each exclosure in 1988, assuming that vegetational

characteristics would have been similar at exclosures and controls in the absence of herbivores. Topography, dominant overstory vegetation, soil characteristics, and moisture levels were considered when selecting control plots.

Stem counts and estimates of ground-cover were inventoried in 1988 on each of 6 exclosures and 12 control sites. The edge area of each exclosure, defined as 1 m from the fence, was excluded from vegetation surveys to eliminate potential browsing by deer from outside and to minimize potential fence effects. Woody plants were defined as stems with active cambium that separated xylem and bark (Cronquist 1982). Woody stems were counted and classified as either shrub-sized or tree-sized by height. Shrubs were defined as stems 0.5 m - 2 m in height, whereas trees were defined as >2 m in height. Height and dbh were also recorded for all trees. Saplings were defined as stems <0.5 m in height; seedlings were tallied separately, and were defined as stems <0.5 m in height that would be totally removed with one incident of browsing.

Stems were tallied by species, except that extremely common species (Gilbert and Harrison 1982a,b), including lowbush blueberry (Vaccinium vacillans, V. angustifolium), lambkill, and wintergreen (Gaultheria procumbens) were excluded. These 3 species were counted in 1.0 x 0.5 m subplots, which were positioned 1 m apart so that >70% of each exclosure was sampled. Seven categories of percent ground-cover were ocularly estimated on the 1.0 x 0.5 m subplots. The categories were grass, herbaceous, fern, moss, organic material (e.g. dead stumps and snags), inorganic material (e.g. rocks), and woody plants < 5 cm in height.

The Student's-t test was used to compare stem densities, mean dbh, and mean tree height between each pair of control sites. If there were no significant difference between the 2 controls, then data for both controls were pooled and compared with the

adjacent enclosure. Because of potential biases associated with site variability independent of browsing, pairs of control sites that differed significantly in density, dbh, or height were omitted from analyses.

A utilization index (UI) was used to determine browsing intensity by deer, using 232 random plots (2 x 25 m) that were surveyed along approximately 100 km of transects throughout ANP (Saeki 1991).

The utilization index was defined as:

$$UI = \frac{\sum_{i=0}^4 (\text{browsing class } i) \times (\# \text{ stems in class } i)}{\text{total number of stems available,}}$$

where browsing classes were: 0 = no browsing, 1 = less than 25%, 2 = 25 - 50%, 3 = 50 - 75%, and 4 = greater than 75% of twigs browsed.

Browsing effects were difficult to separate from site variability because control plots were not established at the time of enclosure construction, and because no post-enclosure data were available. Therefore, we assumed that browsing effects on overall plant species size, composition and density would be reflected by common differences among 6 enclosure and control comparisons.

The percent ground cover in 7 cover categories was compared between enclosure and control plots using a Mann-Whitney U-test (Zar 1984). A Kolmogorov-Smirnov goodness of fit was used to test whether the categorized percentages of ground cover were distributed differently between the enclosure and the pooled estimate for paired control sites (Zar 1984).

A 2 x 4 contingency table (Zar 1984) was used to test whether the height distribution of heavily and lightly utilized species differed between enclosures and controls. Heavily utilized species were defined as the 10 species with the highest UI values for deer,

whereas lightly utilized species were defined as the 10 species with the lowest UI values for deer on MDI (Saeki 1991). When $\geq 20\%$ of expected values were ≤ 5 , log-likelihood ratios were used instead of Chi-square analyses (Zar 1984).

Chi-square analyses or log-likelihood ratios using 2 x 2 contingency tables were also used to test whether the numbers of heavily utilized species and lightly utilized species were independent of deer browsing. These analyses included separate height classes for shrubs and trees.

RESULTS AND DISCUSSION

Hardwood-dominated exclosures on MDI (Breakneck Brook and Precipice) did not differ in species composition and density of plants from their associated controls. However, the exclosures within white cedar dominated habitats on MDI (Aunt Betty Pond and Upper Hadlock Pond) differed from adjacent control plots in species composition, height distribution, and species-specific density. The exclosures on IH (Eli Creek and Long Pond) also differed from control plots in species composition and density. However, no sites that appeared visually suitable as control sites were found near the Long Pond exclosure; therefore, its quantitative comparison may have little meaning. The differences in stem density and species richness between the Eli Creek exclosure and control plots may result from intense browsing on IH where deer and hares have both occurred in high densities for many years (Klataske 1968, Gilbert and Harrison 1982b).

There were no significant differences in tree height or dbh between exclosures and pooled controls (Table 1). Also, species richness appeared to be similar between exclosures and controls, except within the shrub height class. More species in the shrub height class were found in 3 of 6 exclosures; no exclosures had fewer species in the shrub height class than controls. Mean species richness in the shrub height class was 7.67 for 6

exclosures and 5.25 for 12 control plots. Harlow and Downing (1970) concluded that deer browsing did not affect the stem density or species composition of seedlings and sprouts; however, browsing significantly reduced mean tree height. In contrast, Marquis (1981) reported that species composition differed between exclosures and controls, and stem densities of larger trees (>1.5 m in height) were significantly higher within exclosures; however, no significant differences in overall stem densities were observed.

Browsing may retard plant growth rate, or plants may respond with compensatory growth after browsing. Both Harlow and Downing (1970) and Marquis (1981) suggested that height of plants was a major factor influencing vulnerability to browsing, especially for young trees. Therefore, height distribution may indicate browsing effects better than mean height and dbh, because trees (>2 m) are plants that have escaped browsing and have reached a size (height and dbh) class where susceptibility to browsing is greatly reduced.

We observed significant differences ($P < 0.001$) between exclosures and controls in height distribution for heavily utilized species, except at the Long Pond site ($0.05 < P < 0.10$; Table 2). Seedlings occurred less frequently within exclosures, whereas shrub-sized stems occurred more frequently within exclosures. Differences in height distribution for lightly utilized species were significant between exclosure and controls at 3 of 6 sites; however, no consistent patterns were apparent (Table 2).

If a seed or root source is available, the number of seedlings is probably dependent on shading and substrate rather than on the direct effects of deer browsing. Seedlings are protected under the snow from deer browsing during winter. Therefore, the number of shrub-sized stems of heavily utilized species showed the most prominent effects of browsing (Table 2). Within the shrub height class, stem counts of heavily utilized species and lightly utilized species differed between exclosures and controls ($\chi^2 = 15.80 -$

534.07, $P < 0.001$), except for the sites at Hadlock Pond ($\chi^2 = 3.26$, $0.05 < P < 0.10$) and Eli Creek ($G = 2.20$, $0.10 < P < 0.25$). Numbers of heavily utilized and lightly utilized trees ($\chi^2 = 6.22 - 304.11$, $P < 0.025 - 0.001$) also differed significantly between exclosures and controls at 3 of 6 sites.

Using pooled Chi-square values among exclosures and controls at 6 sites, the numbers of shrub-sized stems of heavily utilized and lightly utilized species varied significantly among sites (Heterogeneity $\chi^2 = 145.628$, $P < 0.001$). However, the numbers of shrub-sized stems of heavily utilized and lightly utilized species were more homogeneous among the 3 sites on the burned areas (Aunt Betty, Breakneck, and Precipice exclosures; Heterogeneity $\chi^2 = 5.301$, $P > 0.05$). In summary, the effects of deer browsing were most prominent and consistent for shrub-sized stems of heavily utilized species that occurred in areas burned during the 1947 fire.

The most obvious differences between exclosure and controls were at the Aunt Betty and Upper Hadlock Pond sites, which occurred within the white cedar-bog associations. Highbush blueberry was more numerous on controls, but more white cedar, white birch, and winterberry shrubs grew within the exclosures. The different fire history of these two sites appeared to influence the distribution of height classes of white cedar (Fig. 1). On the unburned area (Upper Hadlock), greater densities of cedar trees, regenerating saplings ($t = 2.155$, $P < 0.05$), and seedlings ($t = 1.823$, $P < 0.10$) were counted outside the exclosure (Fig. 1). In contrast, on the burned area (Aunt Betty) most cedars outside of the exclosure were eliminated due to browsing. Deer browsing pressure became severe during the 1950's and early 1960's when the deer population erupted throughout MDI (McLaughlin 1968). Severe browsing lasted through the mid 1960's and apparently further restricted the regeneration of cedar (McLaughlin 1968). Some cedar trees escaped from

browsing in unburned areas because they were out of reach of deer prior to the deer population increase. However, the scarcity of parent trees resulting from past overbrowsing probably has eliminated the regeneration of cedar on some burned sites, whereas regeneration appears to have resumed on unburned areas.

Successional stage and vegetation type were the two most important factors influencing the effects of browsing. Frelich and Lorimer (1985) stated that browsing effects may be insignificant on forests with a unimodal diameter distribution caused by extensive natural disturbance. The two post-fire exclosure sites within even-aged hardwood stands showed little effects of browsing on density, species composition, tree height, and dbh, whereas the burned white-cedar habitat association showed significant effects of browsing on forest structure and composition.

On all 3 exclosure sites within burned areas, a greater ground cover of ferns was observed ($P < 0.05$) within exclosures (Table 3). Grass, moss, herbaceous, and woody ground cover was also greater ($P < 0.05$) within exclosures at 2 of 3 burned sites. No patterns in ground cover of fern, moss, grass, herbaceous, or woody plants ($P > 0.05$) were apparent on unburned areas. Ground cover changes as understory and overstory vegetation change (Sydes and Grime 1981), possibly resulting from shading and ground litter originating from understory and overstory vegetation. Observed differences in ground cover were the most obvious at the Aunt Betty Pond exclosure site, where tree density inside the exclosure was 4.1 - 7.6 times greater than the two associated control plots. In addition to direct effects of herbivory during snow-free seasons, microclimatic changes (Brand and Goets 1986), trampling (Bobek et al. 1979), and fecal and urine deposition (Watt 1981, Day and Detling 1990) may also affect ground cover in areas exposed to heavy browsing pressure.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

White-tailed deer affect the diversity and size class distribution of preferred browse species. These effects are most prominent in the shrub height class; therefore, browse surveys may be most efficient when directed at highly utilized species of woody plants 0.5 - 2.0 meters in height.

Overall, there were no apparent differences in stem densities, mean height, or dbh of trees among exclosures and controls; therefore, browsing may affect forage supply more significantly than commercial wood production under the range of deer densities studied. Research is needed for other areas of the Northeast with a greater range of deer densities to determine whether browsing ultimately results in reduced production of commercial sized trees.

Browsing effects on species composition, stem densities, and height distribution appear to be more prevalent in white cedar habitats than in hardwood habitats. Within two white cedar-dominated stands, browsing essentially eliminated cedar regeneration on a burned site, whereas browsing effects were much less prominent on an unburned site.

Habitats dominated by aspens and birches that regenerated on burned sites exhibited the least effects of browsing. Extensive regeneration of deciduous root sprouts on large burned areas may dilute the influence of herbivores, even at high densities. These results support the conclusion of Frelich and Lorimer (1985) that browsing effects may be insignificant in forests with a unimodal size distribution following extensive disturbance.

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Table 1. Comparison of mean ($\pm$ SE) dbh (cm) and height (m) of tree species (≥ 6 stems) between exclosure and control plots in Acadia National Park, Maine, 1988.

Parameter	Site	Dominant Species	Exclosure	Control1	Control2	t	P
DBH	Breakneck	white birch	4.6 $\pm$ 0.31	5.2 $\pm$ 0.31	6.5 $\pm$ 0.54	a	
		red maple	6.7 $\pm$ 1.07	6.5 $\pm$ 0.91	6.8 $\pm$ 0.51	0.372 ^b	P > 0.50
	Precipice	white birch	5.0 $\pm$ 0.30	4.5 $\pm$ 0.42	5.6 $\pm$ 0.30	a	
		red oak	11.6 $\pm$ 1.05	11.5 $\pm$ 1.56	15.4 $\pm$ 1.88	0.534 ^b	P > 0.50
	Hadlock	white cedar	6.5 $\pm$ 0.69	6.3 $\pm$ 0.50	4.1 $\pm$ 0.59	a	
		larch ^c	5.1 $\pm$ 0.77	4.6 $\pm$ 0.98	5.7 $\pm$ 0.73	0.173 ^b	P > 0.50
Height	Breakneck	white birch	7.3 $\pm$ 0.35	8.3 $\pm$ 0.28	9.3 $\pm$ 0.50	a	
		red maple	8.7 $\pm$ 0.88	9.1 $\pm$ 0.89	8.8 $\pm$ 0.54	0.224 ^b	P > 0.50
	Precipice	white birch	6.1 $\pm$ 0.29	5.5 $\pm$ 0.40	6.6 $\pm$ 0.24	a	
		red oak	8.5 $\pm$ 0.42	8.4 $\pm$ 0.62	10.3 $\pm$ 0.70	0.552 ^b	P > 0.50
	Hadlock	white cedar	3.4 $\pm$ 0.69	3.3 $\pm$ 0.14	4.1 $\pm$ 0.19	1.049 ^b	P > 0.20
		larch ^c	4.0 $\pm$ 0.42	3.9 $\pm$ 0.50	4.5 $\pm$ 0.49	0.482 ^b	P > 0.50

^a There was a significant difference ($P < 0.05$) between control plots; therefore, no comparisons were made between exclosure and controls.

^b Represents comparison of pooled data for 2 control plots with adjacent exclosure.

^c (*Larix laricina*).

Table 2. A comparison of the number of stems of heavily utilized species^a (HU) and lightly utilized species^b (LU), by height class^c, between exclosure and control plots in Acadia National Park, Maine, 1988.

Site	HU						LU					
	seed	sap	shrub	tree	χ^2	P	seed	sap	shrub	tree	χ^2	P
Breakneck												
Exclosure	93	93	35	55			10	1	2	0		
Controls	232	112	6	78	41.1	P < 0.001	38	10	8	6	3.33 ^d	P > 0.25
Precipice												
Exclosure	190	39	4	57			1	0	0	0		
Controls	589	139	0	106	20.9 ^d	P < 0.001	11	23	10	3	2.84 ^d	P > 0.25
Aunt Betty												
Exclosure	68	110	649	398			0	1	6	13		
Controls	20	117	10	20	426.2	P < 0.001	3	72	86	73	12.1 ^d	P < 0.01
Hadlock Pond												
Exclosure	58	373	135	27			10	23	7	0		
Controls	643	1360	69	109	300.1	P < 0.001	11	31	9	1	1.35 ^d	P > 0.50

Table 2. (continued)

Site	HU						LU					
	seed	sap	shrub	tree	χ^2	P	seed	sap	shrub	tree	χ^2	P
Eli Creek												
Exclosure	268	2	1	13			125	94	5	13		
Controls	1630	2	0	11	27.4 ^d	$P < 0.001$	881	159	11	21	95.0	$P < 0.001$
Long Pond												
Exclosure	6	8	15	102			207	29	28	26		
Controls	2	0	0	2	7.27 ^d	$P < 0.10$	207	17	58	39	14.6	$P < 0.025$

^a Highly utilized species were defined as 10 species with the highest utilization index (UI) values for deer (Saeki 1991).

^b Lightly utilized species were defined as 10 species with the lowest UI values for deer (Saeki 1991).

^c Seedlings = seed; Saplings = sap.

^d A G^2 statistic (log-likelihood ratio) is presented instead of χ^2 because $\geq 20\%$ of expected values were ≤ 5 .

Table 3. A comparison of mean ground cover (%) between exclosures (excl.) and control (ctrl.) sites^a in Acadia National Park, Maine, 1988.

Cover type	BURNED AREAS						UNBURNED AREAS					
	Breakneck		Aunt Betty		Precipice		Hadlock		Eli Creek		Long Pond	
	Excl.	Ctrl.	Excl.	Ctrl.	Excl.	Ctrl.	Excl.	Ctrl.	Excl.	Ctrl.	Excl.	Ctrl.
fern	15.8*	9.9	10.0*	11.1	5.6*	1.6	0	0	5.6*	0.2	1.7*	42.1
grass	0.1	0.4	0.5*	20.4	5.6*	18.5	23.3	31.8	3.3	3.7	0.8	2.0
moss	4.7	5.4	53.0*	20.8	12.7*	2.7	88.5*	94.4	42.3	48.3	3.7	4.9
herb	3.1*	1.4	0.9*	4.6	6.5	7.3	4.1	4.5	9.4*	7.0	3.8*	1.0
organic	1.8*	3.3	8.4*	14.8	5.1	4.8	1.8	2.3	2.9*	7.8	1.7	3.6
Inorganic	3.0*	4.5	1.0	0.8	0.2*	0	0	0	0	0.1	4.2	4.2
woody	22.2*	4.9	0.8*	6.7	3.4	5.2	0	0.1	2.4*	0.1	0.5	2.8

^a Represents a comparison of each exclosure with the pooled data for 2 adjacent control sites.

* Denotes a significant difference ($P < 0.05$) in percent ground cover between exclosure and pooled control sites (Mann-Whitney U-test).

Figure 1. A comparison of stem densities (stems/100 m²), by height class, between exclosures and control sites located in burned (Aunt Betty) and unburned (Upper Hadlock Pond) areas in Acadia National Park, Maine, 1988.

