ARCTIC
VOL. 54, NO. 4 (DECEMBER 2001) P. 407–417

Comparative Effects on Plants of Caribou/Reindeer, Moose and White-Tailed Deer Herbivory

MICHEL CRÊTE,[1] JEAN-PIERRE OUELLET[2] and LOUIS LESAGE[3]

(*Received 15 May 2000; accepted in revised form 21 February 2001*)

ABSTRACT. We reviewed the literature reporting negative or positive effects on vegetation of herbivory by caribou/reindeer, moose, and white-tailed deer in light of the hypothesis of exploitation ecosystems (EEH), which predicts that most of the negative impacts will occur in areas where wolves were extirpated. We were able to list 197 plant taxa negatively affected by the three cervid species, as opposed to 24 that benefited from their herbivory. The plant taxa negatively affected by caribou/reindeer (19), moose (37), and white-tailed deer (141) comprised 5%, 9%, and 11% of vascular plants present in their respective ranges. Each cervid affected mostly species eaten during the growing season: lichens and woody species for caribou/reindeer, woody species and aquatics for moose, and herbs and woody species for white-tailed deer. White-tailed deer were the only deer reported to feed on threatened or endangered plants. Studies related to damage caused by caribou/reindeer were scarce and often concerned lichens. Most reports for moose and white-tailed deer came from areas where wolves were absent or rare. Among the three cervids, white-tailed deer might damage the most vegetation because of its smaller size and preference for herbs.

Key words: caribou, forage, herbivory, moose, reindeer, vegetation, white-tailed deer, wolf

RÉSUMÉ. À la lumière de l'hypothèse de l'exploitation des écosystèmes (EEH), nous avons examiné les publications qui mentionnent les effets négatifs ou positifs, sur la végétation, du broutement du caribou/renne, de l'orignal et du cerf de Virginie. Cette hypothèse prédit que les impacts négatifs se concentrent dans des endroits où le loup a été éliminé. Nous avons pu énumérer 197 taxons végétaux affectés négativement par les trois cervidés, contre 24 qui profitaient du broutement. Le nombre de taxons végétaux affectés négativement par le broutement du caribou/renne (19), de l'orignal (37) et du cerf de Virginie (141) représentait respectivement 5, 9 et 11 p. cent des plantes vasculaires situées dans les aires de répartition spécifiques des animaux. Chaque cervidé affectait surtout les espèces consommées durant la saison de croissance végétale: lichens et plantes ligneuses pour le caribou/renne, plantes ligneuses et aquatiques pour l'orignal, et plantes herbacées et ligneuses pour le cerf de Virginie. Selon les rapports, ce dernier était le seul cerf qui broutait des plantes menacées ou en voie de disparition. Les études rapportant des dommages causés par le caribou/renne étaient rares et traitaient souvent des lichens. La plupart des rapports sur l'orignal et le cerf de Virginie couvraient des zones où le loup était rare ou absent. Des trois cervidés, celui qui causerait le plus de dommages à la végétation est le cerf de Virginie, en raison de sa taille plus petite et de sa préférence pour les plantes herbacées.

Mots clés: caribou, cerf de Virginie, herbivore, loup, nourriture, orignal, renne, végétation

Traduit pour la revue Arctic par Nésida Loyer.

INTRODUCTION

Ecologists and plant physiologists have devoted considerable attention to the impact on vegetation of large herbivores, particularly because they capture proportionally more energy than small herbivores do in terrestrial ecosystems (Silva and Downing, 1995). At the individual and species level, controlled studies have considered plant responses to herbivory in terms of biomass, components, and morphology. Tissue loss can stimulate plant production under some conditions (de Mazancourt et al., 1998), although repeated herbivory often reduces plant biomass. In woody species, plant consumption during the growing season generally reduces production (Hjältén et al., 1993; Canham et al., 1994; Ouellet et al., 1994; Bergström and Danell, 1995; Manseau, 1996; Crête and Doucet, 1998), whereas most of these species can tolerate browsing during dormancy (Aldous, 1952; Krefting et al., 1966; Danell and Bergström, 1989; Hjältén et al., 1993; Canham et al., 1994). Herbivory can modify the chemical composition of plants: hypotheses suggest that some compounds, such as phenolics and terpenoids, represent one of the major mechanisms of woody plant defence against herbivores, although current hypotheses cannot adequately predict plant

[1] Société de la Faune et Parcs du Québec, Direction de la recherche sur la faune, 675 boul. René-Lévesque Est (BP 92), Québec, Québec G1R 5V7, Canada, and Département de biologie, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada, and Département de biologie, Université du Québec à Rimouski, 300, Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada; michel.crete@fapaq.gouv.qc.ca
[2] Département de biologie, Université du Québec à Rimouski, 300, Allée des Ursulines, Rimouski, Québec G5L 3A1, Canada
[3] Département de biologie and Centre d'études nordiques, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada

biochemical responses to tissue loss (Koricheva et al., 1998). Herbivory often induces change in the morphology of woody species that may facilitate or hinder future plant consumption (Krefting et al., 1966; Willard and McKell, 1978; Danell and Bergström, 1989; Edenius, 1993; Danell et al., 1994; McLaren, 1996).

At the community level, Caughley (1976) proposed a simple model describing trophic interactions of plants and ungulates, which applies at an ecological time scale. This model predicts reduction and dampened oscillations of plant (and herbivore) biomass after the colonization of a virgin area by ungulates. More recently, the impact of white-tailed deer (*Odocoileus virginianus*) herbivory in predator-free areas has led some authors to suggest that herbivore/plant systems could have two stable steady-state equilibria, one at high and the other at low plant density (Schmitz and Sinclair, 1997; Stromayer and Warren, 1997; Augustine et al., 1998). Extending a hypothesis put forward by Hairston et al. (1960), Oksanen et al. (1981) proposed a model which predicts trophic interactions along gradients of productivity at an evolutionary time scale: the hypothesis of exploitation ecosystems (EEH; see also Oksanen and Oksanen, 2000). According to the EEH, food chains would be reduced to plants and herbivores in unproductive areas, i.e., those producing less than 700 g per m^2 per year, a level of productivity that corresponds to the transition between the boreal forest and the tundra along a latitudinal gradient (Oksanen et al., 1981). Vegetation would then have evolved under strong grazing pressure in unproductive areas. In more productive landscapes, the EEH predicts that predators would have regulated herbivores, relaxing in turn the grazing pressure on plants; thus plants would have been regulated by competition for light, nutrients, and water. In addition, a trade-off would exist for herbivores in productive ecosystems between predator elusion and forage quality, herbivores selecting nutrient-rich forage to minimize digestive tract weight and to maximize agility (Oksanen, 1992). According to the EEH, the removal of predators from productive areas would cause herbivores to be regulated by competition for forage. This would result in strong grazing pressure, particularly on nutrient-rich plants, i.e., community-wide trophic cascades. Although the existence of community-wide trophic cascades has not yet been shown in terrestrial ecosystems, a meta-analysis indicates that trophic cascades represent a common outcome of predator removal at the species level (Schmitz et al., 2000).

North America is an appropriate continent for testing the EEH because natural predators of large mammals have persisted with relatively limited human interference over its northern half. The current distribution of biomass of cervids, the dominant group of large herbivores in North America (Crête, 1999), supports the EEH. In the High Arctic (> 75˚N), cervid biomass reaches only 0.7 kg per km^2. This figure increases to 16 kg per km^2 on the southern islands of the Canadian Arctic Archipelago (between ≈ 70˚N and 75˚N), and to 106 kg per km^2 in the continental Northwest Territories and northern Québec, where the large Canadian herds of migratory caribou are located. Farther south, in more productive systems, cervid biomass averages 62 kg per km^2 throughout the boreal and mixed forests of Canada where gray wolves (*Canis lupus*) and bears (*Ursus americanus*, *U. arctos*) have remained present, but 299 kg per km^2 at the same latitudes when wolves are absent or recolonizing (Crête, 1999). Similar or higher biomasses of free-ranging cervids occur in Fennoscandia with insignificant predator numbers (Pullianen, 1980; Skogland, 1986; Sagør et al., 1997; Angelstam et al., 2000). South of the wolf range in North America, cervid biomass shows a direct relationship with primary productivity: densities are highest in the southeast of the continent, where the only cervid present is white-tailed deer (Crête, 1999).

We compared the effects on vegetation from herbivory of three well-studied cervid species: reindeer/caribou (*Rangifer tarandus*), moose (*Alces alces*), and white-tailed deer. Under the assumption of the EEH, we predicted that the occurrence of negative effects of cervid herbivory would be concentrated in areas devoid of natural predators, particularly the gray wolf. Caribou coexist with gray wolves throughout their range except on the Island of Newfoundland and in a few other isolated populations. Moose live in the presence of wolves and bears almost everywhere in Canada west of the St. Lawrence River valley, but not in Newfoundland, the Maritimes, and New England. In the northwestern United States, where wolves are locally recolonizing, they have had a marginal impact on moose for many decades. The ranges of white-tailed deer and wolves overlap only slightly, in southern Canada west of the St. Lawrence River valley. Bears and wolves have been kept at very low density in Fennoscandia for many decades (Pullianen, 1980; Sagør et al., 1997).

METHODS

We searched the literature for studies reporting effects of caribou (reindeer), moose, and white-tailed deer herbivory on vegetation found within their natural distribution, which excluded islands of the South Atlantic. We separated plant species into five groups: lichens and mosses, aquatics, other herbs, woody plants with terminal bud within reach of herbivores (≈ 1.5 to 3 m depending on cervid species and season), and woody plants with terminal bud out of reach. For each reference, we noted by species (or in some cases by genus) whether herbivory (a) had a positive or negative influence on plant attributes (i.e., coverage, height, biomass, density, and survival); (b) caused damage (topping, bark stripping, or death); or (c) threatened plant existence locally. When reports compared browsed and unbrowsed sites, we took only those species for which a significant difference existed; otherwise, we accepted the authors' opinion. We mapped the location of each study area, but considered separately each of multiple publications originating from the same site. To compare the three cervid species on the same basis, we divided the

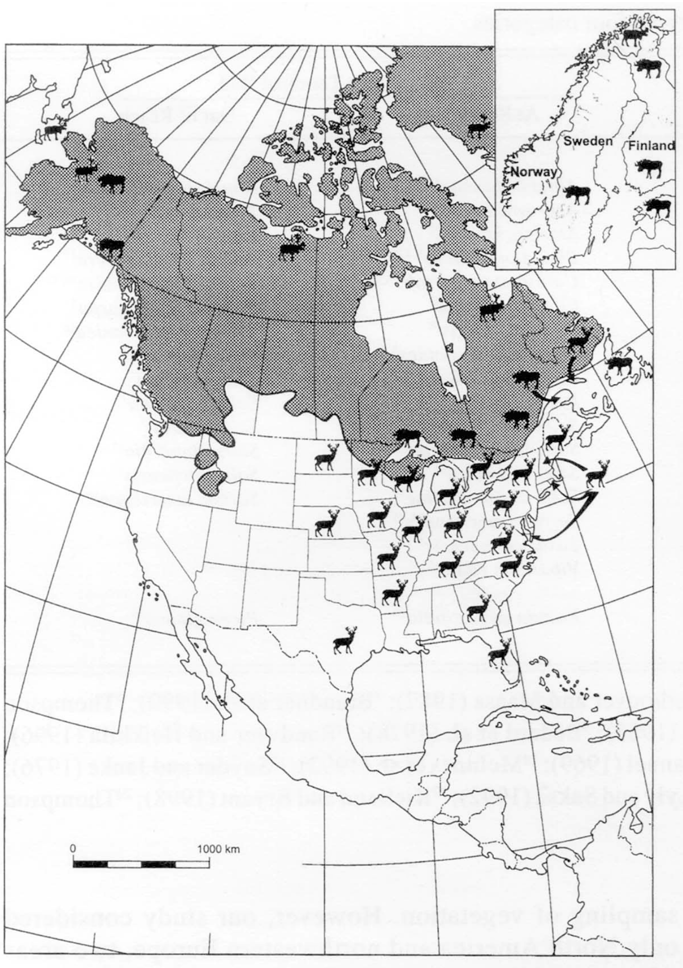

FIG. 1. Location of study areas in which effects of caribou/reindeer, moose and white-tailed deer herbivory on plants were reported. Symbols identify the species (moose facing left, caribou facing right, white-tailed deer facing forward). The shaded area represents the current distribution of the gray wolf in North America.

number of vascular plant species that each cervid negatively affected by the estimated number of plants growing in the centre of its range, taking these estimates from Barthlott et al.'s (1996) map. We selected values of 250 vascular plants within the central range for caribou/reindeer, 400 for moose, and 1250 for white-tailed deer.

RESULTS

We found nine records of caribou/reindeer affecting vegetation from five areas: Alaska, a small island in the Northwest Territories, northern Québec, Greenland, and northern Fennoscandia (Fig. 1). Within the range that moose share with established wolf populations (Fig. 1), we found two reports from Alaska, six from Isle Royale (Michigan), one from Ontario, and one from southern Québec. Outside the wolf range or in lightly populated areas, we found 10 reports, which came from southeastern Québec, Newfoundland, Sweden, Finland, and Estonia. The 25 reports concerning white-tailed deer came from 24

TABLE 1. Number of plant species negatively (or positively) affected by the browsing of three cervid species in North America and Fennoscandia and type of impact on those plant species, as reported in the literature. In some cases, only the genus was specified.

	Caribou/Reindeer	Moose	White-tailed Deer
Trees and Shrubs			
Out of reach	0	14(0)	1(0)
At reach	7(0)	16(2)	46(3)
Herbs			
Terrestrial	5(2)	1(2)	93(5)
Aquatic	0	6(0)	0
Lichens/mosses	7(5)	0	1(0)
Type of Effect			
Coverage	18(5)	0(2)	26(4)
Density	0	9(1)	11(3)
Height	0	14	13(3)
Biomass	7(2)	7(1)	6
Bark/top	0	10	1
Survival	0	7	0
Conservation	0	0	98

TABLE 2. Plants in three broad groups (non-vascular, herbaceous, and woody) negatively or positively affected by caribou/reindeer herbivory, as reported in the literature.

Non-vascular	Herbaceous	Woody
Negative Effects		
Cetraria nivalis[1]	*Eriophorum vaginatum*[2]	*Betula glandulosa*[2, 3, 4]
Cladina arbuscula[7, 8]	*Oxytropis nigrescens*[8]	*Caluna vulgaris*[2, 6]
Cladina stellaris[1, 3, 5, 6]	*Pedicularis sudetica*[8]	*Empetrum nigrum*[2, 3, 6]
Cladina mitis[1]	*Rubus chamaemorus*[3]	*Salix herbacea*[3]
Cladina rangiferina[1]	*Solidago macrophylla*[3]	*Salix planifolia*[3]
Stereocaulon paschale[1]		*Vaccinium vitis-idaea*[3, 6]
Sphagnum sp.[3]		*Vaccinium uliginosum*[2]
Lichens sp.[2, 3, 9]		
Positive Effects		
Cladina arbuscula[5, 6]	*Carex bigelowii*[1]	
Cladina rangiferina[5, 6]	*Festuca ovina*[1]	
Dicranum sp.[5, 6]		
Pleurozium schreberi[6]		
Mosses sp.[2, 3]		

[1] Oksanen (1978); [2]Henry and Gunn (1991); [3]Manseau et al. (1996); [4]Crête and Doucet (1998); [5]Väre et al. (1995); [6]Väre et al. (1996); [7]Pegau (1975); [8]Klein (1987); [9]Thing (1984).

jurisdictions where long-established wolf populations were absent.

Caribou/reindeer, moose, and white-tailed deer negatively affected 19, 37, and 141 plant taxa respectively, as compared to 7, 4, and 8 taxa that took advantage of browsing by the respective cervids (Table 1). Caribou impacted shrubs and lichens/mosses similarly and, to a lesser extent, terrestrial herbs, whereas the majority of plants affected by moose and white-tailed deer were trees/shrubs and herbs, respectively. Caribou and white-tailed deer mostly reduced plant coverage, as opposed to moose, which often reduced plant height and density. With one exception, only moose were reported to be killing some stems and topping and bark stripping trees. White-tailed

TABLE 3. Plants negatively or positively affected by moose herbivory, in four categories.

	Herbaceous		Woody with Terminal Bud	
	Aquatic	Terrestrial	At Reach	Out of Reach
Negative Effects				
	Chara vulgaris[1]	*Aralia nudicaulis*[2]	*Abies balsamea*[3, 4, 5, 6]	*Alnus sinuata*[7]
	Characae sp.[8]		*Acer spicatum*[4, 9]	*Picea abies*[10]
	Nitella flexilis[1]		*Amelanchier* sp.[9]	*Pinus sylvestris*[11, 12]
	Potamogeton alpinus[1, 8]		*Betula papyrifera*[3, 4, 6, 13]	*Populus balsamifera*[17]
	Potamogeton epihydrus[8]		*Cornus stolonifera*[4, 14, 15]	*Populus tremuloides*[16, 17]
	Potamogeton foliosus[8]		*Corylus cornuta*[9]	*Populus trichocarpa*[7]
			Pinus sylvestris[18]	*Prunus pensylvanica*[16]
			Populus tremuloides[3, 4]	*Salix alaxensis*[7]
			Prunus pensylvanica[6]	*Salix barclayi*[7]
			Prunus sp.[14]	*Salix bebbiana*[17]
			Salix alaxensis[19]	*Salix lanata*[17]
			Salix branchycarpa[19]	*Salix planifolia*[17]
			Salix lasiandra[19]	*Salix sitchensis*[7]
			Salix novae-angliae[19]	*Sorbus americana*[16]
			Sorbus americana[14, 15]	
			Taxus canadensis[4, 15]	
			Viburnum edule[15]	
Positive Effects				
		Melampyrum lineare[15]	*Kalmia angustifolia*[20]	*Picea glauca*[15]
		Rubus parviflorus[14]		

[1] Aho and Jordan (1979); [2]Edwards (1985); [3]Pimlott (1963); [4]Risenhoover and Maass (1987); [5]Brandner et al. (1990); [6]Thompson et al. (1992); [7]MacCracken et al. (1997); [8]Fraser and Hristienko (1983); [9]Bédard et al. (1978); [10]Randveer and Heikkilä (1996); [11]Heikkilä (1991); [12]Faber and Thorson (1996); [13]Bergerud and Manuel (1969); [14]McInnes et al. (1992); [15]Snyder and Janke (1976); [16]Desmeules (1968); [17]Miquelle and Van Ballenberghe (1989); [18]Lyly and Saksa (1992); [19]Kielland and Bryant (1998); [20]Thompson and Mallik (1989).

deer were unique in threatening some species, but most cases reported came from a single study based on an interview of state botanists (Miller et al., 1992).

Caribou/reindeer could affect lichens of the genus *Cladina* positively or negatively, depending on browsing pressure (Table 2). Mosses and graminoids often took advantage of caribou herbivory because caribou browsing and trampling can almost completely destroy terrestrial lichens (Thing, 1984; Klein, 1987; Manseau et al., 1996). Two genera were particularly affected by moose, *Potamogeton* among aquatics, and *Salix* among shrubs (Table 3). Moose had very little influence on terrestrial herbs, and very few species benefited from their herbivory. White-tailed deer had a detrimental effect on forest herbs in particular (Table 4), but the importance of their impact might be overestimated, because 80% of the taxa listed came from a single study (Miller et al., 1992). Similarly, 44% of taxa listed for woody plants, the other group impacted by white-tailed deer, were tallied by Miller et al. (1992).

The proportion of vascular plants negatively affected reached 5% for caribou/reindeer, 9% for moose, and 11% for white-tailed deer. However, if we exclude the Miller (1992) study, this last percentage decreases to 3%.

DISCUSSION

Our evaluation of deer herbivory is likely biased because it relied on the literature rather than on a systematic sampling of vegetation. However, our study considered only North America and northwestern Europe, two areas where cervids have received much attention for many decades. We believe that the numerous field ecologists working in North America and Fennoscandia have probably detected most cases of severe impacts of deer herbivory. We argue that our literature review describes at least qualitatively the impact of caribou/reindeer, moose, and white-tailed deer on the ecosystems in which they live.

Overall, caribou/reindeer, moose, and white-tailed deer herbivory caused mostly negative impacts on the vegetation, affecting in particular lichens, shrubs, and terrestrial herbs, respectively (Table 1). The results give some support to our prediction that detrimental effects of cervid herbivory would show up mostly in areas devoid of gray wolves. Reports of vegetation damage caused by caribou/reindeer were limited to a few locations. In Alaska, one report referred to introduced reindeer on St. Matthew Island (Klein, 1987) and the other to Nelchina caribou in the early 1970s (Pegau, 1975). The only report from the Northwest Territories (Henry and Gunn, 1991) concerned an unusual situation: a large group of caribou that remained trapped on a small island after spring breakup of the ice was reduced to starvation. The vegetation recovered soon after this browsing episode. Severe impacts of summer herbivory in northern Québec might also represent a special case because of area geography. On the Québec/Labrador peninsula, the preferred summer habitat of caribou, tundra, covers a much smaller area than their

TABLE 4. Herbaceous and woody plants negatively or positively affected by white-tailed deer herbivory.

Herbaceous	Woody
Negative Effects[a]	
Abronia macrocarpa[1]	*Abies balsamea*[1, 3, 4, 5, 6, 25]
Aconitum noveboracense[1]	*Acer rubrum*[8, 9] *saccharum*[5, 9, 10] *spicatum*[3, 11]
Actaea pachypoda	*Arctostaphylos uva-ursi*[1]
Anemone quinquefolia[7]	*Betula alleghaniensis*[5, 9, 11] *lenta*[9] *papyrifera*[4] *uber*[1]
Angelica atropurpurea[7]	*Chamaecyparis thyoides*[23]
Arabis serotina[1]	*Cornus rugosa*[1]
Aralia nudicaulis[11]	*Corylus cornuta*[3]
Arisaema triphyllum[1, 7, 24]	*Diervilla lonicera*[4]
Asclepias meadii[1] *ovalifolia*[1] *verticillata*[1]	*Dirca palustris*[1]
Astragalus robbinsii[1]	*Evonymus americanus*[1] *atropurpureus*[1] *obovatus*[1]
Chamaelirium luteum[1]	*Fraxinus americana*[1]
Cirsium pitcheri[12, 13]	*Iliamna remota*[1]
Cladrastis lutea[1]	*Larix laricina*[6]
Claytonia virginica[10]	*Lindera melissifolia*[1]
Clematis socialis[1]	*Litsea aestivalis*[1]
Clintonia borealis[11]	*Lonicera polypetala*[1]
Coeloglossum viride[1]	*Mitchella repens*[14]
Corallorrhiza trifida[1]	*Neviusia alabamensis*[1]
Corydalis sempervirens[1]	*Populus grandidentata*[15]
Croomia pauciflora[1]	*Prunus pensylvanica*[3] *pumila*[1] *serotina*[8]
Cypripedium acaule[1] *candidum*[1] *reginae*[1]	*Quercus buckleyi*[22] *ellipsoidalis*[16]
Dalea foliosa[1]	*fusiformis*[22] *macrocarpa*[16]
Delphinium exaltatum[1]	*Rhododendron prunifolium*[1]
Dicentra cucullaria[7, 10]	*Ribes hirtellum*[1]
Erythronium americanum[10]	*Rosa acicularis*[1]
Eupatorium purpureum[1]	*Sorbus americana*[3, 11]
Filipendula rubra[1]	*Styrax texanus*[1]
Gaura neomexicana[1]	*Taxus canadensis*[1,11]
Helianthus microcephalus[1]	*Thuja occidentalis*[6]
Helonias bullata[1]	*Tilia americana*[5]
Hymenocallis sp.[1]	*Torreya taxifolia*[1]
Isotria medeoloides[1] *verticillata*[1]	*Tsuga canadensis*[5, 6, 17, 18, 19]
Lathyrus venosus[16, 26]	*Ulmus rubra*[2]
Lesquerella filiformis[1]	*Virbunum lantanoides*[14]
Liatris scariosa[1]	*Woodwardia virginica*[1]
Lilium canadense[1] *grayi*[1] *iridollae*[1] *philadelphicum*[1]	
Liparis loeselii[1]	
Listera smallii[1]	
Lithospermum caroliniense[1, 20]	
Lobelia kalmii[1]	
Lupinus perennis[1]	
Lysimachia quadriflora[1]	
Maianthemum canadense[7, 11]	
Melanthium latifolium[1] *virginicum*[1]	
Osmorhiza claytonii[24]	
Oxypolis canbyi[1]	
Panax quinquefolius[1]	
Pedicularis furbishiae[1]	
Penstemon haydenii[1] *lemhiensis*[1]	
Plantago cordata[1]	
Platantherea blephariglottis[1] *ciliaris*[1] *cristata*[1]	
flava[1]*grandiflora*[1] *integrilabia*[1] *leucophaea*[1]	
peramoena[1] *praeclara*[1] *psycodes*[1]	
Pycnanthemum torrei[1]	
Sanguinaria canadensis[1]	
Sarracenia oreophila[1] *purpurea*[1]	
Saxifraga micranthidifolia[1]	
Schwalbea americana[1]	
Silene polypetala[1]	
Spiranthes diluvialis[1] *ochroleuca*[1]	
Thalictrum cooleyi[1]	
Trifolium reflexum[1] *stoloniferum*[1]	
Trillium cernuum[1] *cuneatum*[1] *decumbens*[1]	
grandiflorum[1, 7] *persistens*[1] *pusillum*[1] *reliquum*[1] *rugelii*[1] sp.[21]	
Uvularia perfoliata[7]	
Viola macloskeyi[14] sp.[7, 10]	

TABLE 4. Herbaceous and woody plants negatively or positively affected by white-tailed deer herbivory – *continued:*

Herbaceous	Woody
Positive Effects	
Berberis thunbergii[7]	*Acer pensylvanicum*[9]
Dennstaedtia punctilobula[14]	*Fagus grandifolia*[8, 9]
Dryopteris intermedia[14]	*Prunus serotina*[9]
Stellaria media[7]	

[a] also one moss species: *Hyperzia lucidula*[14].

[1] Miller et al. (1992); [2]bark stripping: Fuller and Michael (1993); [3]Pimlott (1963); [4]Potvin and Breton (1992); [5]Anderson and Katz (1993); [6]van Deelen et al. (1996); [7]Koh et al. (1996); [8]Marquis (1981); [9]Tilghman (1989); [10]Riemenschneider et al. (1995); [11]Balgooyen and Waller (1995); [12]Phillips and Maun (1995); [13]Phillips and Maun (1996); [14]Rooney and Dress (1997); [15]Prachar and Samuel (1988); [16]Ritchie et al. (1998); [17]Long et al. (1998); [18]Anderson and Loucks (1979); [19]Frelich and Lorimer (1985); [20]Cambell (1993); [21]Augustine and Frelich (1998); [22]Russel and Fowler (1999); [23]Zampella and Lathrop (1997); [24]Webster and Parker (2000); [25]Cornett et al. (2000); [26]Knops et al. (2000).

winter habitat, forest-tundra and boreal forest (Crête and Huot, 1993). Finally, supplementary feeding in winter may have imposed an artificially high browsing pressure on the vegetation used by reindeer in Fennoscandia (Kumpula et al., 1998). It is noteworthy that we found no mention of herbivory effects on vegetation in the range of the large migratory herds in northwestern Canada and Alaska, where caribou density has been high in recent years (Ferguson and Gauthier, 1992). The crucial impact of caribou on lichens and the slow recovery of this vegetation (e.g., Klein, 1987) make plausible the hypothesis of a long-term, cyclic/fluctuating dynamic (Messier et al., 1988). Cyclic dynamics also characterize populations of small mammals (Turchin and Hanski, 1997) and snowshoe hares (*Lepus americanus*: Boutin et al., 1995) at the same latitudes.

Our results generally support our prediction for moose and white-tailed deer (Fig. 1). Within the wolf range, the two cases involving moose in Alaska (Miquelle and Van Ballenberghe, 1989; MacCracken et al., 1997) and the one in southern Québec (DesMeules, 1968) concerned bark stripping, a feeding behaviour with limited effects on plants (Faber and Edenius, 1998) that can be observed at low population density (DesMeules, 1968). Reports of negative effects of moose herbivory on Isle Royale, where gray wolves occur, would depend on moose being regulated by forage competition, in the absence of black bears. The combined action of wolf and bear species is needed to regulate moose by predation (Crête, 1987; Messier, 1994; Crête, 1999). The last study reporting negative effects of moose herbivory in the wolf range dealt with aquatic feeding in Ontario (Fraser and Hristienko, 1983). Many studies reported negative effects of moose and white-tailed deer herbivory from areas with few (Fennoscandia) or no wolves. However, agriculture might act as a confounding factor in the case of white-tailed deer because some crops help to sustain deer populations (e.g., Nixon et al., 1991), and crop browsing increases the browsing pressure on native plants growing in adjacent woodlots (Augustine and Frelich, 1998).

Deer Impact What They Eat During the Growing Season

During summer, caribou/reindeer consume mostly leaves of shrubs, graminoids, and some herbs, although they continue to eat lichens (Skogland, 1984; Thing, 1984; Gauthier et al., 1989; Crête et al., 1989). Graminoids are very resilient to grazing (e.g., Manseau, 1996). This resilience, as well as their low palatability (Crête et al., 1989), explains the absence of reports on detrimental effects of caribou herbivory for this group. During the snow-free period, trampling by caribou, as well as consumption, might contribute to extirpation of lichens. During the rest of the year, snow cover offers some protection from trampling, though caribou do form craters in the snow to search for food. Moose include mostly leaves of woody plants and some aquatics in their summer diet, but eat very few herbs (Cushwa and Coady, 1976; Morow, 1976; Belovsly, 1981; Crête and Jordan, 1981; Irwin, 1985; Butler, 1986). White-tailed deer consume a broad variety of food items during the growing season according to availability, but in forested areas, they concentrate their browsing on leaves of woody plants, herbs, and grass (Healy, 1971; McCaffery et al., 1974; Skinner and Telfer, 1974; McCullough, 1985; Rose and Harder, 1985; Johnson et al., 1995).

On the basis of the crude list of plant taxa that we present, we should conclude that white-tailed deer have a greater detrimental impact on the vegetation than do caribou/reindeer or moose. In addition, only white-tailed deer pose a risk for rare plant species. White-tailed deer prefer many herb species, in particular lilies and orchids (Miller et al., 1992), and herbs might be less resistant to repeated defoliation than woody species, being more exposed to complete defoliation. White-tailed deer herbivory could also cause the greatest negative impact by reason of relative body size. Given equal forage quality, the smallest cervid should be capable of positive foraging at the lowest plant biomass per surface area (Illius and Gordon, 1987), which means that white-tailed deer (male = 66 kg; Crête and Daigle, 1999) could extirpate a plant species from an area more easily than could moose (442 kg) or caribou/reindeer (159 kg).

Can Deer Herbivory Change the Structure of Plant Communities?

In the absence of predators, moose and white-tailed deer herbivory could convert forests into scrubland or chaparral after perturbation if they browsed down all tree and shrub species. Two case studies illustrate the mechanisms that prevent such an outcome: Potvin and Breton (1992) for white-tailed deer and McInnes et al. (1992) for moose.

White-tailed deer on Anticosti Island in the Gulf of St. Lawrence have controlled all palatable herbs, deciduous woody plants (Potvin and Breton, 1992), and balsam fir regeneration even in large clear-cut areas (> 1 km^2: F. Potvin, pers. comm. 1999). However, white and black spruce (*Picea glauca*; *P. mariana*) receive very little browsing (Huot, 1982). Balsam fir has dominated the forests growing on this island until recently, but white spruce is likely replacing it; in the future, the island should remain treed, but forest composition should change drastically unless deer density declines significantly. Moose on Isle Royale in Lake Superior affect the vegetation in a similar manner, although their summer browsing concentrates on woody species. Moose reduce the leaf biomass of deciduous trees and shrubs, reduce their height, slow down canopy closure by deciduous trees, and favour herbs by letting more light reach the ground (McInnes et al., 1992). In addition, winter browsing on balsam fir postpones canopy closure by this species (McLaren and Peterson, 1994). However, moose rarely browse spruce, and Isle Royale should remain forested under the worst-case scenario; until recently, moose had not impeded paper birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) from growing out of their reach (McInnes et al., 1992).

At high caribou/reindeer population density, tundra plants could be at risk of extirpation since they all remain within the reach of herbivores. However, such plant communities appear to tolerate browsing well. Manseau et al. (1996) illustrate this point. Caribou in northern Québec have almost extirpated lichens, but their effect on vascular plants has remained more limited, only reducing the leaf biomass of some shrub species. For instance, their browsing has not destroyed stands of dwarf birch (*Betula glandulosa*), their preferred forage (Crête et al., 1989), although it has affected the health of stems (Crête and Doucet, 1998). The relative resilience of the tundra vegetation to caribou/reindeer browsing could result from coevolution at relatively high herbivore density, as suggested by the EEH.

Although deer herbivory cannot change the structure of ecosystems in an ecological time frame, it can substantially modify their plant composition and biomass. Browsing could threaten or eliminate some species: in particular, herbs could be threatened by white-tailed deer (Miller et al., 1992). This possibility exists (Crête, 1999), but local or total elimination should generally be improbable for at least two reasons. Woody species and herbs react to defoliation in various ways that often reduce the efficiency of future herbivory because of size reduction (e.g., Balgooyen and Waller, 1995; Crête and Doucet, 1998). This reaction can produce a feedback in the herbivore by lowering its physical condition, fecundity, and population density, relaxing pressure on the vegetation. In addition, refugia exist for plants to escape herbivory, i.e., cliffs, inaccessible plateaux (Manseau et al., 1996), boulders (Rooney, 1997), and treefall mounds (Long et al., 1998). We conclude that the standing biomass of preferred forage species can be drastically reduced by deer herbivory, but that most taxa should persist during periods of high herbivory and should recolonize vacant areas when deer density decreases, a plausible possibility after severe forage reduction or reintroduction of natural predators (Crête, 1999). On an evolutionary time scale, the permanent exclusion of predators could allow the appearance (particularly in forests) of herbivores adapted to exploit nutrient-poor forage (e.g., spruce; Oksanen, 1992). In such a case, one should expect major changes in the structure and the composition of plant communities. Areas where large carnivores have been extirpated in recent times may currently represent coevolutionary hot spots (sensu Thompson, 1999).

We cannot conclude firmly whether the body of data collected to date on plant/herbivore interactions for these three cervid species supports the EEH. However, measuring cervid biomass and annual forage production along a productivity gradient would provide a powerful test of the hypothesis. Indeed, the EEH predicts that, in the absence of functional predators, the standing biomass of herbivores would increase along with primary productivity, whereas that of forage would remain constant or show a very modest increase (Oksanen and Oksanen, 2000). This test could be carried out in eastern North America, from the tip of the Gaspé Peninsula to Florida. It would involve measuring cervid biomass and standing forage biomass at the end of a normal growing season in natural areas where moose and white-tailed deer have not been strongly limited by hunting during previous decades.

ACKNOWLEDGEMENTS

We would like to express our gratitude to L. Oksanen and F. Potvin, who kindly commented on a previous draft of this manuscript. D. J. Currie indicated the reference that included a map showing the density of vascular plants on the earth's surface. The Société de la Faune et des Parcs du Québec, the Fonds FCAR, and NSERC supported this work.

REFERENCES

AHO, R.W., and JORDAN, P.A. 1979. Production of aquatic macrophytes and its utilization by moose on Isle Royale National Park. In: Linn, R.M., ed. Proceedings of the First Conference on

Scientific Research in National Parks. U.S. Department of Interior, National Park Service, Transactions and Proceedings Series 5. 341–348.

ALDOUS, S.E. 1952. Deer browse clipping study in the Lake States region. Journal of Wildlife Management 16:401–409.

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

ANDERSON, R.C., and LOUCKS, O.L. 1979. White-tailed deer (*Odocoileus virginianus*) influence on structure and composition of *Tsuga canadensis* forests. Journal of Applied Ecology 16: 855–861.

ANGELSTAM, P., WIKBERG, P.-E., DANILOV, P., FABER, W.E., and NYGRÉN, K. 2000. Effects of moose density on timber quality and biodiversity restoration in Sweden, Finland, and Russian Karelia. Alces 36:133–145.

AUGUSTINE, D.J., and FRELICH, L.E. 1998. Effects of white-tailed deer on populations of an understory forb in fragmented deciduous forests. Conservation Biology 12:995–1004.

AUGUSTINE, D.J., FRELICH, L.E., and JORDAN, P.A. 1998. Evidence for two alternate stable states in an ungulate grazing system. Ecological Applications 8:1260–1269.

BALGOOYEN, C.P., and WALLER, D.M. 1995. The use of *Clintonia borealis* and other indicators to gauge impacts of white-tailed deer on plant communities in northern Wisconsin, USA. Natural Areas Journal 15:308–318.

BARTHLOTT, W., LAUER, W., and PLACKE, A. 1996. Global distribution of species diversity in vascular plants: Towards a world map of phytodiversity. Erdkunde 50:317–327.

BÉDARD, J., CRÊTE, M., and AUDY, E. 1978. Short-term influence of moose upon woody plants of an early seral wintering site in Gaspé Peninsula, Québec. Canadian Journal of Forest Research 8:407–415.

BELOVSKY, G.E. 1981. Food plant selection by a generalist herbivore: The moose. Ecology 62:1020–1030.

BERGERUD, A.T., and MANUEL, F. 1969. Moose damage to balsam fir-white birch forests in central Newfoundland. Journal of Wildlife Management 32:729–746.

BERGSTRÖM, R., and DANELL, K.1995. Effects of simulated summer browsing by moose on leaf and shoot biomass of birch, *Betula pendula*. Oikos 72:132–138.

BOUTIN, S., KREBS, C.J., BOONSTRA, R., DALE, M.R.T., HANNON, S.J., MARTIN, K., SINCLAIR, A.R.E., SMITH, J.N.M., TURKINGTON, R., BLOWER, M., BYROM, A. DOYLE, F.I., DOYLE, C., HIK, D., HOFER, L., HUBBS, A., KARELS, T., MURRAY, D.L., NAMS, V., O'DONOGHUE, M., ROHNER, C., and SCHWEIGER, S. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada's boreal forest. Oikos 74:69–80.

BRANDNER, T.A., PETERSON, R.O., and RISENHOOVER, K.L. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. Ecology 71:155–164.

BUTLER, C.E. 1986. Summer food utilization and observations of a tame moose, *Alces alces*. Canadian Field-Naturalist 100: 85–88.

CAMPBELL, J.M. 1993. Effects of grazing by white-tailed deer on a population of *Lithospermum caroliniense* at Presque Isle. Journal of the Pennsylvania Academy of Science 67:103–108.

CANHAM, C.D., McANINCH, J.B., and WOOD, D.M. 1994. Effects of the frequency, timing, and intensity of simulated browsing on growth and mortality of tree seedlings. Canadian Journal of Forest Research 24:817–825.

CAUGHLEY, G. 1976. Wildlife management and the dynamics of ungulate populations. In: Coaker, T.H., ed. Applied biology, Vol. 1. London: Academic Press. 183–246.

CORNETT, M.W., FRELICH, L.E., PUETTMANN, K.J., and REICH, P.B. 2000. Conservation implications of browsing by *Odocoileus virginianus* in remnant upland *Thuya occidentalis* forests. Biological Conservation 93:359–369.

CRÊTE, M. 1987. The impact of sport hunting on North American moose. Swedish Wildlife Research, Supplement 1:553–563.

———. 1999. The distribution of deer biomass in North America supports the hypothesis of exploitation ecosystems. Ecology Letters 2: 223–227.

CRÊTE, M., and DAIGLE, C. 1999. Management of indigenous North American deer at the end of the 20th century in relation to large predators and primary production. Acta Veterinaria Hungarica 47:1–16.

CRÊTE, M., and DOUCET, G.J. 1998. Persistent suppression in dwarf birch after release from heavy summer browsing by caribou. Arctic and Alpine Research 30:126–132.

CRÊTE, M., and HUOT, J. 1993. Regulation of a large herd of migratory caribou: Summer nutrition affects calf growth and body reserves of dams. Canadian Journal of Zoology 71: 2291–2296.

CRÊTE, M., and JORDAN, P.A. 1981. Régime alimentaire des orignaux du sud-ouest québécois pour les mois d'avril à octobre. Canadian Field-Naturalist 95:50–56.

CRÊTE, M., HUOT, J., and GAUTHIER, L. 1989. Food selection during early lactation by caribou calving on the tundra in Québec. Arctic 43:60–65.

CUSHWA, C.T., and COADY, J. 1976. Food habits of moose, *Alces alces*, in Alaska: A preliminary study using rumen contents analysis. Canadian Field-Naturalist 90:11–16.

DANELL, K., and BERGSTRÖM, R. 1989. Winter browsing by moose on two birch species: Impact on food resources. Oikos 54:11–18.

DANELL, K., BERGSTRÖM, R., and EDENIUS, L. 1994. Effects of large mammalian browsers on architecture, biomass, and nutrients of woody plants. Journal of Mammalogy 75:833–844.

DE MAZANCOURT, C., LOREAU, M., and ABBADIE, L. 1998. Grazing optimization and nutrient cycling: When do herbivores enhance plant production? Ecology 79:2242–2252.

DESMEULES, P. 1968. Notes on the use of bark by moose (*Alces alces americana* Clinton) in Laurentide park (Québec). Naturaliste Canadien 95:1159–1164.

EDENIUS, L. 1993. Browsing by moose on Scots pine in relation to plant resource availability. Ecology 74:2261–2269.

EDWARDS, J. 1985. Effects of herbivory by moose on flower and fruit production of *Aralia nudicaulis*. Journal of Ecology 73: 861–868.

FABER, W.E., and EDENIUS, L. 1998. Bark stripping by moose in commercial forests of Fennoscandia—a review. Alces 34: 261–268.

FABER, W.E., and THORSON, E.M. 1996. Bark stripping of young *Pinus sylvestris* by *Alces alces* on the individual, stand, and landscape level in Sweden. Canadian Journal of Forest Research 26:2109–2114.

FERGUSON, M.A.D., and GAUTHIER, L. 1992.Status and trends of *Rangifer tarandus* and *Ovibos moschatus* populations in Canada. Rangifer 12:127–141.

FRASER, D., and HRISTIENKO, H. 1983. Effects of moose, *Alces alces*, on aquatic vegetation in Sibley Provincial Park, Ontario. Canadian Field-Naturalist 97:57–61.

FRELICH, L.E., and LORIMER, C.G. 1985. Current and predicted long-term effects of deer browsing in hemlock forests in Michigan, USA. Biological Conservation 34:99–120.

FULLER, J.C., and MICHAEL, E.D. 1993. Bark stripping of slippery elm by white-tailed deer. Northeast Science 50:101–110.

GAUTHIER, L., NAULT, R., and CRÊTE, M. 1989. Variations saisonnières du régime alimentaire des caribous du troupeau de la rivière George, Québec nordique. Naturaliste Canadien 116:101–112.

HAIRSTON, N.G., SMITH, F.E., and SLOBODKIN, L.B. 1960. Community structure, population control, and competition. American Naturalist 94:421–424.

HEALY, W.M. 1971. Forage preferences of tame deer in a northwest Pennsylvania clear-cutting. Journal of Wildlife Management 35:717–723.

HEIKKILÄ, R. 1991. Moose browsing in a Scots pine plantation mixed with deciduous tree species. Acta Forestalia Fennica 224:1–13.

HENRY, G.H.R., and GUNN, A. 1991. Recovery of tundra vegetation after overgrazing by caribou in Arctic Canada. Arctic 44:38–42.

HJÄLTÉN, J., DANELL, K., and ERICSON, L. 1993. Effects of simulated herbivory and intraspecific competition on the compensatory ability of birches. Ecology 74:1136–1142.

HUOT, J. 1982. Body condition and food resources of white-tailed deer on Anticosti Island, Québec. Ph.D. thesis, University of Alaska, Fairbanks.

ILLIUS, A.W., and GORDON, I.J. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology 56: 989–999.

IRWIN, L.L. 1985. Foods of moose, *Alces alces*, and white-tailed deer, *Odocoileus virginianus*, on a burn in boreal forest. Canadian Field-Naturalist 99:240–245.

JOHNSON, A.S., HALE, P.E., FORD, W.M., WENTWORTH, J.M., FRENCH, J.R., ANDERSON, O.F., and PULLEN, G.B. 1995. White-tailed deer foraging in relation to successional stage, overstory type and management of southern Appalachian forests. American Midland Naturalist 133:18–35.

KIELLAND, K., and BRYANT, J.P. 1998. Moose herbivory in taiga: Effects on biogeochemistry and vegetation dynamics in primary succession. Oikos 82:377–383.

KLEIN, D.R. 1987. Vegetation recovery patterns following overgrazing by reindeer on St. Matthew Island. Journal of Range Management 40:336–338.

KNOPS, J.M.H., RITCHIE, M.E., and TILMAN, D. 2000. Selective herbivory on a nitrogen fixing legume (*Lathyrus venosus*) influences productivity and ecosystem nitrogen pools in an oak savanna. Écoscience 7:166–174.

KOH, S., WATT, T.A., BAZELY, D.R., PEARL, D.L., TANG, M., and CARLETON, T.J. 1996. Impact of white-tailed deer (*Odocoileus virginianus*) on plant community composition. Aspects of Applied Biology 44:445–450.

KORICHEVA, J., LARSSON, S., HAUKIOJA, E., and KEINÄNEN, M. 1998. Regulation of woody plant secondary metabolism by resource availability: Hypothesis testing by means of meta-analysis. Oikos 83:212–226.

KREFTING, L.W., STENLUND, M.H., and SEEMEL, R.K. 1966. Effect of simulated and natural deer browsing on mountain maple. Journal of Wildlife Management 30:481–488.

KUMPULA, J., COLPAERT, A., and NIEMINEN, M. 1998. Reproduction and productivity of semidomesticated reindeer in northern Finland. Canadian Journal of Zoology 76:269–277.

LONG, Z.T., CARSON, W.P., and PETERSON, C.J. 1998. Can disturbance create refugia from herbivores: An example with hemlock regeneration on treefall mounds. Journal of the Torrey Botanical Society 125:165–168.

LYLY, O., and SAKSA, T. 1992. The effect of stand density on moose damage in young *Pinus sylvestris* stands. Scandinavian Journal of Forest Research 7:393–403.

MacCRACKEN, J.G., VAN BALLENBERGHE, V., and PEEK, J.M. 1997. Habitat relationships of moose on the Copper River Delta in coastal south-central Alaska. Wildlife Monographs 136:1–52.

MANSEAU, M. 1996. Relation réciproque entre les caribous et la végétation des aires d'estivage: Le cas du troupeau de la rivière George. Ph.D. thesis, Université Laval.

MANSEAU, M., HUOT, J., and CRÊTE, M. 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: Community and landscape level. Journal of Ecology 84:503–513.

MARQUIS, D.A. 1981. Effects of deer browsing on timber production in Allegheny hardwood forests of northwestern Pennsylvania. U.S. Department of Agriculture, Forest Service, Research Paper NE-475.

McCAFFERY, K.R., TRANETZKI, J., and PIECHURA, J., Jr., 1974. Summer foods of deer in northern Wisconsin. Journal of Wildlife Management 38:215–219.

McCULLOUGH, D.R. 1985. Variables influencing food habits of white-tailed deer on the George Reserve. Journal of Mammalogy 66:682–692.

McINNES, P.F., NAIMAN, R.J., PASTOR, J., and COHEN, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. Ecology 73:2059–2075.

McLAREN, B.E. 1996. Plant-specific response to herbivory: Simulated browsing of suppressed balsam fir on Isle Royale. Ecology 77:228–235.

McLAREN, B.E., and PETERSON, R.O. 1994. Wolves, moose, and tree rings on Isle Royale. Science 266:1555–1558.

MESSIER, F. 1994. Ungulate population models with predation: A case study with the North American moose. Ecology 75: 478–488.

MESSIER, F., HUOT, J., LeHÉNAFF, D. and LUTTICH, S. 1988. Demography of the George River Caribou Herd: Evidence of population regulation by forage exploitation and range expansion. Arctic 41:279–287.

MILLER, S.G., BRATTON, S.P., and HADIDIAN, J. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. Natural Areas Journal 12:67–74.

MIQUELLE, D.G., and VAN BALLENBERGHE, V. 1989. Impact of bark stripping by moose on aspen-spruce communities. Journal of Wildlife Management 53:577–586.

MOROW, K. 1976. Food habits of moose from Augustów forest. Acta Theriologica 21:101–116.

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

OKSANEN, L. 1978. Lichen grounds of Finnmarksvidda, northern Norway, in relation to summer and winter grazing by reindeer. Kevo Subarctic Research Station 14:64–71.

———. 1992. Evolution of exploitation ecosystems I. Predation, foraging ecology and population dynamics in herbivores. Evolutionary Ecology 6:15–33.

OKSANEN, L., and OKSANEN, T. 2000. The logic and realism of the hypothesis of exploitation ecosystems. American Naturalist 155:703–723.

OKSANEN, L., FRETWELL, S.D., ARRUDA, J., and NIEMELA, P. 1981. Exploitation ecosystems in gradients of primary productivity. American Naturalist 118:240–261.

OUELLET, J.-P., BOUTIN, S., and HEARD, D.C. 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. Canadian Journal of Zoology 72:1426–1435.

PEGAU, G.R. 1975. Analysis of the Nelchina caribou range. Proceedings of the First International Reindeer/Caribou Symposium. 316–323.

PHILLIPS, T.D., and MAUN, M.A. 1995. The ecological impact of white-tailed deer on Pitcher's thistle (*Cirsium pitcheri*): A rare plant species. American Journal of Botany 82 (Supplement 6):54–55.

———. 1996. Population ecology of *Cirsium pitcheri* on Lake Huron sand dunes. I. Impact of white-tailed deer. Canadian Journal of Botany 74:1439–1444.

PIMLOTT, D.H. 1963. Influence of deer and moose on boreal forest vegetation in two areas of eastern Canada. International Union of Game Biologists Congress 6:106–116.

POTVIN, F., and BRETON, L. 1992. Impact du cerf de Virginie sur la succession végétale après coupe à Anticosti: suivi d'un ensemble d'exclos de 1984 à 1989. Ministère du Loisir, de la Chasse et de la Pêche, report SP 1932-05-92.

PRACHAR, R.E., and SAMUEL, D.E. 1988. Influence of white-tailed deer browsing on mortality and growth of regenerating aspen. Transactions of the Northeast Section of the Wildlife Society 45:27–36.

PULLIANEN, E. 1980. The status, structure and behaviour of populations of the wolf (*Canis l. lupus* L.) along the Fenno-Soviet border. Annales Zoologici Fennici 17:107–112.

RANDVEER, T., and HEIKKILA, R. 1996. Damage caused by moose (*Alces alces* L.) by bark stripping of *Picea abies*. Scandinavian Journal of Forest Research 11:153–158.

RIEMENSCHNEIDER, V., CORDELL, T.B., and ALLISON, B. 1995. Impact of white-tailed deer on plant cover and biomass in Potato Creek State Park, St. Joseph County, Indiana. Proceedings of the Indiana Academy of Science 104:35–41.

RISENHOOVER, K.L., and MAASS, S.A. 1987. The influence of moose on the composition and structure of Isle Royale forests. Canadian Journal of Forest Research 17:357–364.

RITCHIE, M.E., TILMAN, D., and KNOPS, J.M.H. 1998. Herbivore effects on plant nitrogen dynamics in oak savanna. Ecology 79:165–177.

ROONEY, T.P. 1997. Escaping herbivory: Refuge effects on the morphology and shoot demography of the clonal forest herb *Maianthemum canadense*. Journal of the Torrey Botanical Society 124:280–285.

ROONEY, T.P., and DRESS, W.J. 1997. Species loss over sixty-six years in the ground-layer vegetation of Heart's Content, an old-growth forest in Pennsylvania, USA. Natural Areas Journal 17:297–305.

ROSE, J., and HARDER, J.D. 1985. Seasonal feeding habits of an enclosed high density white-tailed deer herd in northern Ohio. Ohio Academy of Science 85:184–190.

RUSSEL, F.L., and FOWLER, N.L. 1999. Rarity of oak sampling in savannas and woodlands of the eastern Edwards Plateau, Texas. Southwestern Naturalist 44:31–41.

SAGØR, J.T., SWENSON, J.E., and RØSKAFT, E. 1997. Compatibility of brown bear *Ursus arctos* and free-ranging sheep in Norway. Biological Conservation 81:91–95.

SCHMITZ, O.J., and SINCLAIR, A.R.E. 1997. Rethinking the role of deer in forest ecosystem dynamics. In: McShea, W.J., Underwood, H.B., and Rappole, J.H., eds. The science of overabundance: Deer ecology and population management. Washington, D.C.: Smithsonian Institution Press. 201–223.

SCHMITZ, O.J., HAMBÄCK, P.A., and BECKERMAN, A.P. 2000. Trophic cascades in terrestrial systems: A review of the effects of carnivore removals on plants. American Naturalist 155:141–153.

SILVA, M., and DOWNING, J.A. 1995. The allometric scaling of density and body mass: A nonlinear relationship for terrestrial mammals. American Naturalist 145:704–727.

SKINNER, W.R., and TELFER, E.S. 1974. Spring, summer, and fall foods of deer in New Brunswick. Journal of Wildlife Management 38:210–214.

SKOGLAND, T. 1984. Wild reindeer foraging-niche organization. Holarctic Ecology 7:345–379.

———. 1986. Density dependent food limitation and maximal production in wild reindeer herds. Journal of Wildlife Management 50:314–319.

SNYDER, J.D., and JANKE, R.A. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. American Midland Naturalist 95:79–92.

STROMAYER, K.A.K., and WARREN, R.J. 1997. Are overabundant deer herds in the eastern United States creating alternate stable states in forest plant communities? Wildlife Society Bulletin 25:227–234.

THING, H. 1984. Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. Danish Review of Game Biology 12:1–52.

THOMPSON, I.D., and MALLIK, A.U. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. Canadian Journal of Forest Research 19:524–526.

THOMPSON, I.D., CURRAN, W.J., HANCOCK, J.A., and BUTLER, C.E. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. Forest Ecology and Management 47:29–37.

THOMPSON, J.N. 1999. Specific hypotheses on the geographic mosaic coevolution. American Naturalist 153 (supplement): S1–S14.

TILGHMAN, N.G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. Journal of Wildlife Management 53:524–532.

TURCHIN, P., and HANSKI, I. 1997. An empirically based model for latitudinal gradient in vole population dynamics. American Naturalist 149:842–874.

VAN DEELEN, T.R., PREGITZER, K.S., and HAUFLER, J.B. 1996. A comparison of presettlement and present-day forests in two northern Michigan deer yards. American Midland Naturalist 135:181–194.

VÄRE, H., OHTONEN, R., and OKSANEN, J. 1995. Effects of reindeer grazing on understorey vegetation in dry *Pinus sylvestris* forests. Journal of Vegetation Science 6:523–530.

VÄRE, H., OHTONEN, R., and MIKKOLA, K. 1996. The effect and extent of heavy grazing by reindeer in ologtrophic pine heaths in northeastern Fennoscandia. Ecography 19:245–253.

WEBSTER, C.R., and PARKER, C.R. 2000. Evaluation of *Osmorhiza claytonii* (Michx.) C.B. Clarke, *Arisaema triphyllum* (L.) Schott, and *Actea pachypoda* Ell. as potential indicators of white-tailed deer overabundance. Natural Areas Journal 20: 176–188.

WILLARD, E.E., and McKELL, C.M. 1978. Response of shrubs to simulated browsing. Journal of Wildlife Management 42: 514–519.

ZAMPELLA, R.A., and LATHROP, R.G. 1997. Landscape changes in Atlantic white cedar (*Chamaecyparis thyoides*) wetlands of the New Jersey Pinelands. Landscape Ecology 12:397–408.