Influence of repeated fertilization on forest ecosystems: relative habitat use by mule deer and moose

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Abstract: This study was designed to test the hypothesis that large-scale precommercial thinning (PCT) and repeated fertilization of young lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) stands would enhance relative habitat use by mule deer (*Odocoileus hemionus* Rafinesque) and moose (*Alces alces* L.) in summer and winter periods, compared to that in mature and old-growth stands. Replicate study areas were located near Summerland, Kelowna, and Williams Lake in south central British Columbia, Canada. Each study area had a range of PCT densities, with and without fertilization, and mature and old-growth stands. Habitat use in summer and winter was measured by pellet-group counts of deer and moose from 1999 to 2003, 6–10 years after the onset of treatments. During summer months, habitat use by deer was enhanced by PCT with fertilization, and the 1000 stems/ha fertilized stands experienced greater use than the unthinned or mature stands. Winter habitat use by deer was similar in the 1000 stems/ha fertilized stands and old-growth stands. In both summer and winter, moose preferred fertilized to unfertilized stands and low-density to high-density stands. Intensive management of young lodgepole pine forests has considerable potential to develop summer and winter ranges for these ungulates.

Résumé : Cette étude visait à tester l'hypothèse que l'éclaircie précommerciale (ÉPC) à grande échelle et la fertilisation à répétition de jeunes peuplements de pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) peuvent faire augmenter l'utilisation relative de l'habitat, en été et en hiver, par le cerf mulet (*Odocoileus hemionus* Rafinesque) et l'orignal (*Alces alces* L.), comparativement aux peuplements matures et aux vieux peuplements. Les répétitions des aires d'étude étaient situées près de Summerland, Kelowna et Williams Lake dans le centre sud de la Colombie-Britannique, au Canada. Chaque aire d'étude avait une gamme de densités d'ÉPC avec et sans fertilisation, ainsi que des peuplements matures et des vieux peuplements. L'utilisation de l'habitat en été et en hiver a été mesurée par comptage de tas de fèces de cerf et d'orignal de 1999 à 2003, soit 6 à 10 ans après le début des traitements. En été, l'utilisation relative de l'habitat par le cerf était plus élevée dans les ÉPC fertilisées; les peuplements de 1000 tiges/ha fertilisés ont été plus utilisés que les peuplements non éclaircis ou matures. En hiver, l'utilisation de l'habitat par le cerf était semblable dans les peuplements de 1000 tiges/ha fertilisés et les vieux peuplements. En été comme en hiver, l'orignal préférait les peuplements fertilisés aux peuplements non fertilisés et ceux de faible densité par rapport à ceux de plus forte densité. L'aménagement intensif de jeunes forêts de pin tordu latifolié offre un potentiel considérable pour le développement des quartiers d'été et d'hiver de ces ongulés.

[Traduit par la Rédaction]

Introduction

A critical component of sustainable forest management is provision of year-round habitats for all wildlife species. One of the most important factors driving timber supply reviews in the southern interior of British Columbia, and elsewhere in the Pacific Northwest, is maintenance of winter ranges for ungulates. In particular, in areas of relatively high snowpack, both mule deer (*Odocoileus hemionus* Rafinesque) and moose (*Alces alces* L.) seem to require mature and old-growth forest stands with high levels of crown closure for snow interception during winter months (Armleder et al. 1994; Balsom et al. 1996). In addition, these old forests often provide the best winter range conditions because they intercept snow and supply forage via herbs, shrubs, and arboreal lichen and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) litterfall (Dawson et al. 1990; Nyberg 1990).

The question of the relative proportions of old forest cover and availability of forage for ungulate winter ranges has generated much controversy, particularly in those areas where severe winters (and high snowfalls) are infrequent. Consequently, understanding the influence of maximizing the availability of preferred forage species on ungulate habitat use should be an integral component of adaptive management of winter ranges. Fire suppression over the past several

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Table 1. Experimental design for experiments A and B.

(*a*) Experiment A.

	250 stems/ha		500 stems/ha		1000 stems/ha		2000 stems/ha		
Replicate[a]	T	T + F	T	T + F	T	T + F	T	T + F	Unthinned
1	A	B	C	D	E	F	G	H	I
2	A	B	C	D	E	F	G	H	I
3	A	B	C	D	E	F	G	H	I

(*b*) Experiment B.

Replicate[b]	Young plantation	T[c]	T[c] + F	Unthinned	Mature	Old growth
1	Y_1	T_1	TF_1	U_1	M_1	OG_1
2	Y_2	T_2	TF_2	U_2	M_2	OG_2
3	Y_3	T_3	TF_3	U_3	M_3	OG_3

Note: T, thinned; F, fertilized.
[a]Replicate 1, Summerland study area; replicate 2, Kelowna study area; replicate 3, Cariboo study area.
[b]Replicate 1, Kelowna study area (medium sites); replicate 2, Kelowna study area (wet sites); replicate 3, Summerland study area.
[c]Precommercially thinned to 1000 stems/ha.

decades has resulted in many overstocked coniferous forests covering vast areas of the Pacific Northwest (Fiedler and Carlson 1992). Because there is an inverse relationship between rooted forage and forest canopy cover, it is perhaps not surprising that increasing forest cover and declining forage have been linked to a presumed long-term decline in abundance of mule deer in parts of western North America (Peek et al. 2001, 2002).

Perhaps the greatest potential to enhance forest understory vegetation is silvicultural management of young stands by precommercial thinning (PCT) and fertilization. PCT contributes to both volume and quality increases in wood fibre on those crop trees selected for superior growth and form during stand thinning (Johnstone 1985), and fertilization, particularly with nitrogen, may enhance this effect (Weetman 1988; Brockley et al. 1992). Young lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) forests cover up to 20×10^6 ha in the Pacific Northwest of North America and are amenable to these silvicultural treatments (Koch 1996; Brockley 1996). Biomass responses of understory vegetation to stand thinning (Sullivan et al. 2001; Lindgren et al. 2006) and to fertilization (VanderSchaaf et al. 2000; Sullivan et al., in press) have generally been positive. In addition, these silvicultural tools could be used to accelerate ecosystem development, perhaps creating old-growth structural features in intensively managed stands (Hayes et al. 1997; Sullivan et al. 2001).

Nyberg (1990) discussed the use of thinning and fertilization to enhance summer and winter ranges of black-tailed deer (*Odocoileus hemionus columbianus* Zimmermann) in coastal coniferous forests. Lyon (1987) reported on elk (*Cervus elaphus* L.) response to thinning of lodgepole pine stands. In both cases, these ungulates likely responded to the enhanced structural diversity that provided forage and cover. Unfortunately, there is a dearth of studies investigating the responses of understory vegetation and relative habitat use by ungulates, such as mule deer and moose, to a range of PCT densities and fertilization. In particular, there are no reports of the responses in overall stand structure and ungulate habitat use to intensive management (i.e., repeated fertilization) of young stands, with comparison to conditions in older forests.

Thus, this study was designed to test the hypothesis that large-scale stand thinning (PCT) and repeated fertilization, up to 10 years after the onset of treatments, would enhance relative habitat use by mule deer and moose in both summer and winter seasons, compared to that in mature and old-growth stands.

Materials and methods

Experimental design

Two experiments (A and B) were conducted. Each study area used during experiment A was divided into four treatment units, each receiving a randomly assigned PCT treatment of 250, 500, 1000, or 2000 stems/ha. Half of each thinning unit received fertilizer treatments. An unthinned stand completed the experimental design and resulted in a total of nine experimental units (eight treatment stands and one unthinned stand). Assignment of fertilizer treatments was partially dependent on logistics related to the helicopter application method used to deliver the fertilizer and was, therefore, not completely random.

In experiment B (mosaic of habitats), three replicates were chosen at the Kelowna study area (replicate 1: medium sites; replicate 2: wet sites) and Summerland study area (replicate 3). Each mosaic consisted of six habitats that represented the most common habitat types in these particular forest management areas: (1) young plantation; (2) young thinned stand; (3) young thinned and fertilized stand; (4) young unthinned stand; (5) mature stand; and (6) old-growth stand.

An outline of the experimental design for experiments A and B is given in Table 1. Additional details of the PCT and fertilization treatments in experiment A are reported in Sullivan et al. (in press).

Study areas

Experiment A was located in three study areas in southern British Columbia in young lodgepole pine stands that had relatively uniform tree cover, comparable diameter, height, and density of trees prior to stand treatments. The Summerland study area was located in the Bald Range, 25 km west of Summerland in south central British Columbia (49°40′N; 119°53′W). This area is within the Montane Spruce (MS_{dm})

biogeoclimatic zone (Meidinger and Pojar 1991) at an elevation range of 1450–1520 m, with gently rolling topography and sandy loam soil. The MS has a cool, continental climate with cold winters and moderately short, warm summers. Mean annual temperature is 0.5–4.7 °C, and precipitation ranges from 380 to 900 mm.

Clear-cut harvesting of lodgepole pine with some single and group seed-tree reserves of Douglas-fir began in this area in 1978 in response to an outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopk.). Depending on the original composition of the harvested stands and the degree of windthrow after harvesting, the number of residual Douglas-fir ranged from none to 1 or 2 trees/ha in our candidate stands. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species in these young stands. Our study area consisted of three harvested units with prethinning stand densities ranging from 9980 to 11 150 stems/ha. Minor components of the stands included Douglas-fir, interior hybrid spruce (*Picea glauca* (Moench) Voss × *Picea engelmannii* Parry), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), ponderosa pine (*Pinus ponderosa* Dougl. ex P. & C. Laws.), willows (*Salix* spp.), sitka alder (*Alnus sinuata* (Regel) Rydb.), and trembling aspen (*Populus tremuloides* Michx.).

In 1998, at 5 years after the start of treatments and at the initiation of this study, mean (±SE) diameter at breast height (DBH = 1.3 m) ranged from 5.0 ± 0.2 cm to 9.5 ± 0.2 cm, and mean (±SE) stand height ranged from 4.1 ± 0.1 m to 5.1 ± 0.1 m, with a mean age of 17–19 years. Stand areas ranged from 4.4 to 11.3 ha.

The Kelowna study area was located 37 km northwest of Kelowna, British Columbia (50°04′N; 119°34′W) in the MS_{dm} biogeoclimatic subzone. Topography of this area is also gently rolling to flat with sandy loam soil at 1220–1240 m elevation. This area was also clear-cut harvested in 1979–1980 and regenerated naturally to lodgepole pine, with the other coniferous species, including western larch (*Larix occidentalis* Nutt.), as minor components. One large unit (84.8 ha) with a prethinning density of 8686 stems/ha was horseshoe-shaped, with an unharvested riparian buffer zone separating the two arms. This riparian zone had a steep ravine and varied in width from 75 to 300 m. The overall unit was separated into eight treatment stands as per the experimental design. An additional unit (12.6 ha) 0.5 km away was used as the unthinned stand.

In 1998, the mean (±SE) DBH ranged from 6.2 ± 0.2 cm to 10.8 ± 0.2 cm, and mean (±SE) stand height ranged from 5.3 ± 0.1 m to 6.4 ± 0.1 m, with a mean stand age of 17–18 years. Stand areas ranged from 9.5 to 12.6 ha.

The Cariboo study area was located in the Alex Fraser Research Forest (The University of British Columbia), 75 km northeast of Williams Lake, British Columbia (52°29′N; 121°45′W) in the Sub-Boreal Spruce (SBS_{dm}) biogeoclimatic zone (Meidinger and Pojar 1991). While this study area was located in a different zone than the two areas to the south, the MS and SBS zones have many similarities, including comparable mean winter and snow conditions (Meidinger and Pojar 1991). The general topography is gently rolling to flat at 850–870 m elevation. In mature stands, interior hybrid spruce, subalpine fir, and some Douglas-fir are mixed with extensive stands of lodgepole pine, which regenerated after wildfires. This unit covered 80 ha and was clear-cut harvested in 1976, followed by some natural regeneration and some planting of lodgepole pine in 1983. Prethinning stand density was 3333 stems/ha. Eight treatment stands were located on this unit. Paired stands were contiguous on one side only. A ninth treatment unit acted as the unthinned stand as per the experimental design.

In 1998, the mean (±SE) DBH ranged from 8.5 ± 0.2 cm to 12.7 ± 0.3 cm, and mean (±SE) stand height ranged from 6.1 ± 0.1 m to 7.6 ± 0.2 m, with a mean stand age of 18 years. Stand areas ranged from 1.5 to 4.5 ha. These stands were separated by 0.2–0.5 km.

In experiment B, the two young plantations (Y_1 and Y_2) at Kelowna were clear-cut harvested in 1995 and were 13.2 and 9.2 ha, respectively. These plantations regenerated naturally to lodgepole pine. Previous forest cover was 99- to 101-year-old lodgepole pine with mean DBH of 19.5–20.0 cm and mean height of 20.0–20.5 m. The young lodgepole pine stands were precommercially thinned to 1000 stems/ha in 1993 ($T_1$and T_2); precommercially thinned to 1000 stems/ha in 1993 and fertilized in fall 1994, spring 1997, fall periods of 1998, 2000, and spring 2003 (TF_1 and TF_2); and the unthinned stands (U_1 and U_2). These latter stands were clear-cut harvested in 1979 and 1982, respectively, and regenerated naturally to lodgepole pine, with the other coniferous species as minor components.

The mature forest stands (M_1 and M_2) were composed primarily of lodgepole pine, with a minor component of Douglas-fir and interior spruce at 80–120 years of age. Each of these stands was located near the paired young plantation units (Y_1 and Y_2). The old-growth forest stands (OG_1 and OG_2) were in the 140- to 250-year age-class. Stand OG_1 was dominated by Douglas-fir and stand OG_2 by subalpine fir, Douglas-fir, and interior spruce.

At Summerland, the young plantation (Y_3) was clear-cut harvested in winter 1995–1996 and was 12.8 ha. This site was planted with lodgepole pine in spring 1997. Previous forest cover was 140- to 250-year-old lodgepole pine. The young lodgepole pine stands were precommercially thinned to 1000 stems/ha in 1993 (T_3); precommercially thinned to 1000 stems/ha in 1993 and fertilized (in an identical manner to the Kelowna replicates) (TF_3); and unthinned stands (U_3) located on a unit clear-cut harvested in 1978. Lodgepole pine regenerated naturally after harvesting and was the dominant tree species in these stands.

The mature forest stand (M_3) in this replicate was composed primarily of 80- to 120-year-old lodgepole pine, with a minor component of Douglas-fir and subalpine fir. There were some veteran Douglas-fir (140–250 years old) trees dispersed through the stand. The old-growth forest stand (OG_3) had 120- to 140-year-old lodgepole pine and Douglas-fir, with subalpine fir and spruce as minor components. Douglas-fir also occurred throughout the stand in the veteran age class of ≥251 years.

Understory vegetation

Three 25 m transects, consisting of five 5 m × 5 m plots, were systematically located in each stand following the method of Stickney (1980). Each plot contained three sizes of nested subplots: a 5 m × 5 m plot for sampling trees, a 3 m × 3 m subplot for sampling shrubs, and a 1 m × 1 m subplot for

sampling herbs. Classification as herb, shrub, or tree was based on the species, not on plant size. Tree, shrub, and herb layers were subdivided into six height classes: 0–0.25, 0.25–0.5, 0.5–1.0, 1.0–2.0, 2.0–3.0, and 3.0–5.0 m. A visual estimate of percent cover of the ground was made for each species height class combination within the appropriate nested subplot. Total percent cover for each layer was also estimated. These data were then used to calculate crown volume index (m^3/0.01 ha) for each plant species (Stickney 1980). The product of percent cover and representative height gives the volume of a cylindroid, which represents the space occupied by the plant in the community. Crown volume index values were then averaged by species for each plot size and converted to 0.01 ha base to produce a tabular value for each species and layer (herbs, shrubs, and trees). Sampling was done annually in July–August 1999 to 2003, 6–10 years since PCT. Sampling was done by the same person in all years. Grasses were not identified to species. Plant species were identified in accordance with Hitchcock and Cronquist (1973), MacKinnon et al. (1992), and Parish et al. (1996).

Habitat diversity was measured by species richness, the total number of species sampled for the plant (herbs, shrubs, and trees) communities in each stand (Krebs 1999).

Relative habitat use

Sampling of fecal pellet groups was used to measure relative habitat use by mule deer and moose for summer (May to September) and winter (October to April) periods in 1999–2003. We counted all new pellet groups (minimum of 20 pellets per group) on cleared permanent 5 m^2 (r = 1.26 m) circular plots (Loft and Kie 1988; Edge and Marcum 1989). Plots were located systematically, in five-plot arrays installed at stations every 50 m, throughout each stand at the three study areas. Numbers of sample plots per stand ranged from 55 to 145 at Summerland, 60 to 140 at Kelowna, and 35 to 100 at the Cariboo study area in experiment A; numbers of sample plots ranged from 55 to 145 in the three replicate blocks in experiment B. Plots were permanently marked with a flagged aluminum "pig-tail" stake, and a small painted rock was placed in the plot center. Counts of pellet groups used a rope of 1.26 m radius attached to the center stake and rotated around the plot. Plots were cleared of all pellet groups, at the initial sampling times, in early October 1998 (experiment A) and May 1999 (experiment B). To measure overwinter habitat use by deer and moose, pellet group counts commenced in the first 2 weeks of May 1999. Similarly, relative habitat use in summer was measured by counting pellet groups in the first 2 weeks of October. This same procedure was followed for five summer and five (four in experiment B) winter periods, and all sample plots at a given study area were assessed by the same observers throughout the 5 years. Pellet group degradation was not likely an issue, as only new pellets deposited during a given summer or winter period were counted. Pellet groups located on the edge of a sample plot had to have 50% or more of the group within the plot to be counted. This technique, consistency of sampling personnel, and the relatively small edge/area ratio of our plots likely minimized potential inclusion bias. Density of pellet groups was estimated per 5 m^2 plot and then converted to a per-hectare value.

Statistical analysis

In experiment A, a split-split plot analysis of variance (ANOVA) was used to test for significant differences in mean crown volume index of herbs, shrubs, and trees, and mean total species richness of all vascular plants, and for mean number of pellet groups per hectare for mule deer and moose, as a measure of relative habitat use across the nine treatment habitats. The three replicates were treated as random factors (i.e., blocks); the density treatment was assigned as main plot, the fertilizer treatment as split-plot, and time as split-split plot. Before performing any analyses, data not conforming to properties of normality and equal variance were subjected to various transformations to best approximate the assumptions required by any ANOVA (Zar 1999). Where significant density or fertilizer main effects were detected that also had significant time interactions, additional split-plot analyses were conducted within individual years.

In experiment B, a repeated-measures ANOVA was used to test for significant differences in mean crown volume index of herbs, shrubs, and trees, total mean species richness of all vascular plants, and mean number of pellet groups per hectare for mule deer and moose, as a measure of relative habitat use across the six mosaic habitats. The same preanalysis tests were conducted as for the analysis of data for experiment A. Mauchley's W test statistic was used to test for sphericity (independence of data among repeated measures) (Littel 1989; Kuehl 1994).

Overall mean (n = 15; 3 replicates × 5 years) values and 95% confidence intervals (CI) were calculated for the number of pellet groups of deer and moose in the treatment stands during summer and winter periods in experiments A and B. Mean values and 95% CI were based on n = 12 (3 replicates × 4 years) for winter periods in experiment B. In all analyses, the level of significance was at least P = 0.05. When a significant difference was found, the location of the difference was determined using Duncan's multiple range test (DMRT).

Results

Understory vegetation

A detailed summary of specific habitat variables in experiment A (crown volume index of herbs, shrubs, and trees, total species richness, and total structural diversity) is given in Sullivan et al. (in press); the overall vegetation analysis is provided in Sullivan et al.[2]

For experiment A, mean crown volume index of herbs was significantly higher in the fertilized than in the unfertilized stands. Mean crown volume index of shrubs was not affected by treatments, but that of trees was significantly higher in the 2000 stems/ha and unthinned stands than in the other stands. The lower three densities (250, 500, and 1000 stems/ha) had similar mean crown volume indices of trees. Total mean richness of vascular plants was significantly reduced by fertilization.

[2] T.P. Sullivan, D.S. Sullivan, and P.M.F. Lindgren. Influence of repeated fertilization on forest ecosystems: I. Abundance and diversity of understory vegetation. Manuscript in preparation.

Table 2. Mean (n = 3 replicate stands; SE in parentheses) crown volume index of herbs, shrubs, and trees and total species richness within the mosaic of habitats sampled in experiment B and results of repeated measures analysis of variance.

	Stand[a]						Stand		Time		Stand × time	
Species	1	2	3	4	5	6	$F_{[5,10]}$	P	$F_{[4,48]}$	P	$F_{[20,48]}$	P
Volume (m^3/0.01 ha)												
Herbs	bc	bc	a	ab	c	bc	5.31	**0.01**	10.05	**<0.01**	1.18	0.31
1999	7.11	7.43	40.65	24.41	0.18	6.98						
	(1.00)	(0.54)	(18.76)	(6.93)	(0.10)	(3.49)						
2000	16.32	17.72	63.15	27.95	0.36	10.39						
	(1.75)	(3.94)	(24.78)	(3.33)	(0.23)	(5.27)						
2001	14.51	14.86	57.13	27.80	0.33	9.44						
	(1.76)	(2.56)	(25.13)	(7.15)	(0.18)	(5.09)						
2002	12.20	10.34	34.52	16.06	0.24	5.90						
	(3.59)	(0.96)	(14.90)	(1.80)	(0.12)	(3.33)						
2003	9.23	7.96	35.81	16.70	0.20	5.20						
	(2.15)	(0.78)	(18.59)	(3.14)	(0.10)	(2.49)						
Shrubs	ns	ns	ns	ns	ns	ns	1.50	0.27	6.29	**<0.01**	0.82	0.68
1999	2.72	11.51	5.49	14.71	2.30	6.44						
	(0.74)	(4.78)	(1.26)	(8.02)	(0.68)	(2.37)						
2000	4.95	13.98	8.86	16.54	2.93	6.88						
	(0.35)	(5.63)	(1.98)	(8.62)	(0.78)	(1.90)						
2001	7.95	16.04	11.48	18.40	3.56	8.92						
	(1.15)	(4.68)	(3.82)	(9.39)	(0.72)	(2.85)						
2002	9.30	15.82	7.81	14.07	3.74	7.65						
	(2.84)	(4.05)	(1.10)	(7.21)	(1.03)	(1.80)						
2003	8.48	14.77	11.47	14.85	2.78	7.66						
	(1.65)	(4.64)	(3.85)	(8.34)	(0.62)	(2.02)						
Trees	e	d	cd	ab	a	bc	33.65	**<0.01**	18.56	**<0.01**	1.35	0.19
1999	3.22	46.54	57.43	136.73	181.40	137.97						
	(1.83)	(7.62)	(5.86)	(34.25)	(18.29)	(14.90)						
2000	4.40	70.99	90.28	192.63	235.07	152.57						
	(0.30)	(10.63)	(9.77)	(31.14)	(45.63)	(8.73)						
2001	6.82	102.41	134.32	200.61	288.22	198.49						
	(0.77)	(22.41)	(16.59)	(24.85)	(22.84)	(19.86)						
2002	12.11	94.73	119.06	201.97	246.16	165.78						
	(1.34)	(13.96)	(8.55)	(18.46)	(7.36)	(16.44)						
2003	20.52	101.98	149.79	204.06	246.07	141.06						
	(5.21)	(11.28)	(13.12)	(28.08)	(22.46)	(9.93)						
Total species richness												
All plants	ab	ab	ab	a	c	bc	4.44	**0.02**	7.37	**<0.01**	0.82	0.68
1999	17.00	19.67	19.55	20.11	9.88	13.33						
	(2.34)	(0.88)	(0.89)	(1.28)	(1.28)	(2.80)						
2000	18.44	22.00	22.33	23.88	10.66	14.34						
	(2.94)	(1.65)	(0.70)	(2.42)	(1.26)	(2.59)						
2001	17.44	22.33	21.78	22.55	11.67	14.67						
	(2.00)	(1.20)	(1.75)	(2.05)	(1.50)	(2.65)						
2002	18.33	21.00	20.89	21.78	11.22	14.56						
	(2.73)	(1.17)	(2.11)	(2.47)	(1.66)	(2.51)						
2003	17.11	19.11	17.11	20.33	10.89	14.12						
	(3.21)	(1.28)	(2.08)	(1.17)	(1.98)	(2.51)						

Note: Columns of mean values with different letters are significantly different according to Duncan's multiple range test, adjusted for multiple contrasts. ns, not significant.

[a]1, young plantation; 2, thinned (1000 stems/ha); 3, thinned (1000 stems/ha) and fertilized; 4, unthinned; 5, mature; 6, old-growth stand.

For experiment B, mean crown volume index of herbs was significantly different among stands, with the biomass of herbs greatest in the thinned–fertilized stands and lowest in the mature stands ($F_{[5,10]}$ = 5.31; P = 0.01) (Table 2). Shrub volume was similar among stands, and total volume of trees was significantly different ($F_{[5,10]}$ = 33.65; P < 0.01) among stands, as expected (Table 2). Total mean species richness of vascular plants was significantly different ($F_{[5,10]}$ = 4.44; P =

Table 3. Summary of split-split plot ANOVA results (density treatment is main plot, fertilizer treatment is split plot, and time is split-split plot) for mean (n = 3 replicate stands) number of deer fecal pellet groups per hectare for five summers (1999 to 2003) and five winters (1998–1999 to 2002–2003) in experiment A.

(a) Mean (±SE) number of deer fecal pellet groups.

	Density (stems/ha)[a]								
Year	250	250 F	500	500 F	1000	1000 F	2000	2000 F	Unthinned
Summer									
1999	407.9±175.7	488.6±305.9	40.0±40.0	113.3±63.6	164.4±87.8	343.2±189.6	81.6±47.6	171.6±134.2	26.7±17.6
2000	175.5±106.1	613.4±331.9	20.0±20.0	135.0±102.6	168.7±90.6	220.3±101.6	109.8±109.8	238.0±114.3	66.7±29.1
2001	200.0±100.0	686.8±315.7	80.0±60.0	190.0±106.9	155.4±116.5	186.4±135.5	36.9±20.4	77.4±42.3	8.5±8.5
2002	374.9±222.8	1003.9±527.6	53.3±29.1	241.7±131.8	102.5±35.6	414.7±183.7	140.8±72.9	293.6±122.3	40.0±23.1
2003	208.9±134.5	740.1±413.1	53.3±13.3	255.0±118.6	62.4±20.7	252.3±169.7	29.0±9.0	145.5±81.0	26.7±6.7
Winter									
1998–1999	126.7±63.6	315.3±73.6	26.7±17.6	220.0±113.7	120.4±54.0	212.1±126.1	196.5±84.4	353.3±146.2	46.7±6.7
1999–2000	266.0±56.4	289.6±118.1	73.3±35.3	403.3±185.9	104.7±14.8	227.0±95.0	125.9±7.1	394.8±138.3	146.7±87.4
2000–2001	197.8±101.1	239.1±209.8	120.0±50.3	421.7±255.9	252.9±107.0	693.0±373.2	328.8±49.9	506.4±271.8	193.3±17.6
2001–2002	184.4±97.8	531.5±322.8	120.0±46.2	528.3±177.6	317.4±113.3	807.1±374.9	349.0±67.4	541.4±197.2	160.0±11.5
2002–2003	451.7±126.5	578.2±155.4	213.3±127.2	555.0±273.9	456.9±160.2	480.1±249.0	305.1±174.9	403.2±216.2	113.3±76.9

(b) Summary of split-split plot ANOVA results.

	Density		Fertilizer		Density × fertilizer		Time		Density × time		Fertilizer × time	
Season	$F_{[4,8]}$	P	$F_{[1,8]}$	P	$F_{[3,8]}$	P	$F_{[4,72]}$	P	$F_{[16,72]}$	P	$F_{[4,72]}$	P
Summer	1.56	0.27	17.74	**<0.01**	1.29	0.34	2.51	**0.05**	1.75	0.06	0.54	0.71
Winter	1.50	0.29	2.08	0.19	0.92	0.47	2.23	0.07	1.84	**0.04**	0.44	0.78

[a]An "F" following the stem density values indicates that a fertilizer treament was applied.

Fig. 1. Mean (n = 15) number (95% confidence interval) of fecal pellet groups per hectare for mule deer in the nine treatment stands during (*a*) summer and (*b*) winter periods from 1999 to 2003 at the three replicate study areas (experiment A). F, fertilization; Unth, unthinned.

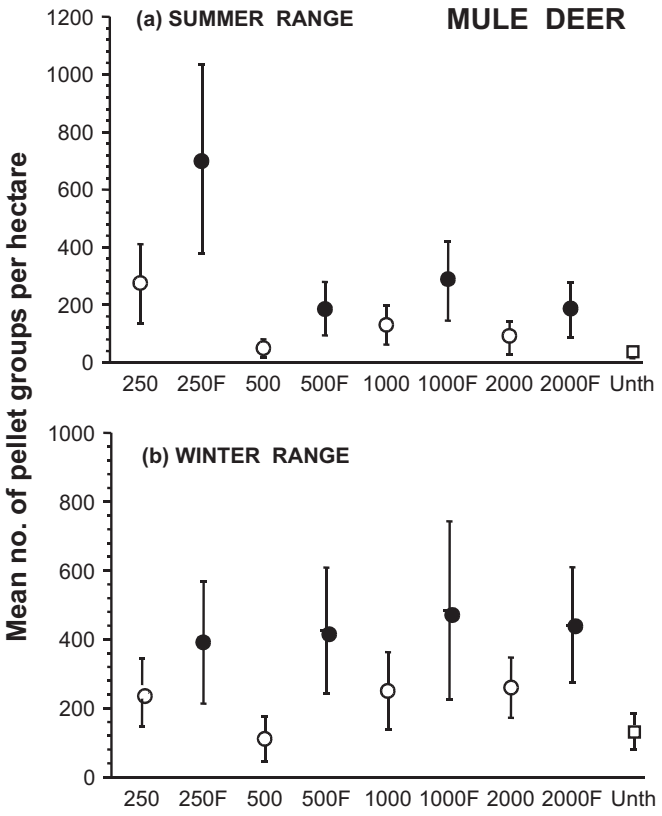
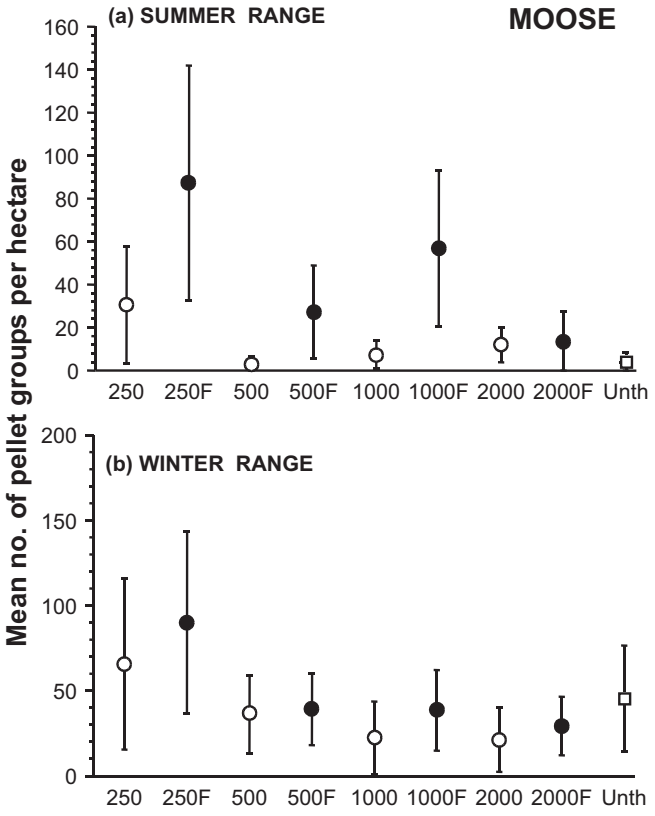


Fig. 2. Mean (n = 15) number (95% confidence interval) of fecal pellet groups per hectare for moose in the nine treatment stands during (*a*) summer and (*b*) winter periods from 1999 to 2003 at the three replicate study areas (experiment A). F, fertilization; Unth, unthinned.



0.02) among stands; total species richness was highest in the young plantation and young pine stands and lowest in the mature stands (Table 2).

Relative habitat use

In experiment A, relative habitat use by deer (based on number of pellet groups per hectare) during summer periods was not affected by density ($F_{[4,8]}$ = 1.56; P = 0.27), but was significantly higher ($F_{[1,8]}$ = 17.74; P < 0.01) in fertilized than in unfertilized stands (Table 3). This latter pattern in overall mean number of pellet groups per hectare was consistent across all four stand densities during summer months (Fig. 1*a*). In winter, relative habitat use by deer was not affected by density ($F_{[4,8]}$ = 1.50; P = 0.29) or fertilization ($F_{[1,8]}$ = 2.08; P = 0.19). However, there was a similar pattern of higher numbers of pellet groups in fertilized than in unfertilized stands (Fig. 1*b*).

Relative habitat use by moose during summer periods was significantly different among treatment stands for density ($F_{[4,8]}$ = 3.80; P = 0.05), with low-density stands being used more (DMRT; P = 0.05) than unthinned stands. Fertilization appeared to enhance habitat use; however, differences were only marginally significant ($F_{[1,8]}$ = 4.68; P = 0.06) (Table 4; Fig. 2*a*). In winter months, moose had similar ($F_{[4,8]}$ = 2.89; P = 0.09) use of stands with respect to density, but had significantly higher ($F_{[1,8]}$ = 7.50; P = 0.03) use of fertilized than of unfertilized stands (Table 4; Fig. 2*b*).

In experiment B, relative habitat use by deer was significantly different ($F_{[5,10]}$ = 4.61; P = 0.02) among stands during summer periods (Table 5; Fig. 3*a*). The thinned–fertilized stands had higher (DMRT; P = 0.05) use by deer than the unthinned or mature stands and comparable use with the other stands (young plantation, thinned, and old growth). Relative habitat use by deer during winter periods also followed this pattern ($F_{[5,10]}$ = 3.16; P = 0.06) (Table 6; Fig. 3*b*).

Relative habitat use by moose was similar (P > 0.05) across stands in these mosaics of habitats in both summer and winter periods (Tables 5 and 6; Fig. 4*a*, 4*b*). Despite these statistical results and the considerable variability among data, the mean number of moose pellet groups per hectare was consistently greater within the thinned–fertilized stands than in any of the other stands. Depending on the year, the thinned–fertilized stands had between 3.4 and 13.7 times higher pellet group densities than the stand with the next highest pellet density. This range was 1.0–1.9 times that for the winter months (Table 6).

Discussion

Relative habitat use

Our study is the first detailed investigation of relative habitat use by mule deer and moose, based on fecal pellet groups, in intensively managed young forests, with a com-

Table 4. Summary of split-split plot ANOVA results (density treatment is main plot, fertilizer treatment is split plot, and time is split-split plot) for mean (n = 3 replicate stands) number of moose fecal pellet groups per hectare for five summers (1999 to 2003) and five winters (1998–1999 to 2002–2003) in experiment A.

(a) Mean (±SE) number of moose fecal pellet groups.

	Density (stems/ha)[a]								
Year	250	250 F	500	500 F	1000	1000 F	2000	2000 F	Unthinned
Summer									
1999	11.1±11.1	19.1±19.1	6.7±6.7	20.0±20.0	0.0±0.0	50.0±50.0	6.7±6.7	26.7±26.7	6.7±6.7
2000	26.7±26.7	136.2±46.5	6.7±6.7	40.0±40.0	18.1±9.7	57.1±11.2	6.7±6.7	13.3±13.3	0.0±0.0
2001	37.8±23.2	138.1±72.1	0.0±0.0	13.3±13.3	12.6±6.4	66.7±66.7	6.7±6.7	0.0±0.0	6.7±6.7
2002	57.1±57.1	119.1±85.8	0.0±0.0	21.7±11.7	0.0±0.0	61.7±36.1	20.0±11.5	26.7±17.6	6.7±6.7
2003	19.0±19.0	23.8±17.2	0.0±0.0	41.7±30.0	7.0±7.0	48.3±38.8	20.0±11.5	0.0±0.0	0.0±0.0
Winter									
1998–1999	41.3±20.8	21.0±12.4	13.3±6.7	28.3±17.4	7.0±7.0	6.7±6.7	26.7±26.7	20.0±11.5	33.3±24.0
1999–2000	19.0±19.0	89.5±41.2	73.3±37.1	30.0±15.3	25.1±12.8	63.8±13.8	13.3±13.3	46.7±29.1	60.0±41.6
2000–2001	106.3±90.2	90.5±49.7	40.0±23.1	40.0±30.6	60.2±44.6	31.7±22.4	0.0±0.0	26.7±13.3	46.7±29.1
2001–2002	76.2±76.2	181.0±99.4	20.0±20.0	66.7±33.3	19.6±12.2	82.1±34.6	46.7±29.1	40.0±23.1	73.3±54.6
2002–2003	86.0±44.8	68.6±27.3	33.3±24.0	30.0±15.3	0.0±0.0	8.3±8.3	20.0±20.0	13.3±13.3	13.3±13.3

(b) Summary of split-split plot ANOVA results.

	Density		Fertilizer		Density × fertilizer		Time		Density × time		Fertilizer × time	
Season	$F_{[4,8]}$	P	$F_{[1,8]}$	P	$F_{[3,8]}$	P	$F_{[4,72]}$	P	$F_{[16,72]}$	P	$F_{[4,72]}$	P
Summer	3.80	**0.05**	4.68	0.06	1.28	0.34	1.13	0.35	0.87	0.60	0.99	0.42
Winter	2.89	0.09	7.50	**0.03**	0.31	0.82	2.27	0.07	1.69	0.07	1.09	0.37

[a]An "F" following the stem density values indicates that a fertilizer treament was applied.

Table 5. Mean (n = 3 replicate stands; SE in parentheses) number of fecal pellet groups per hectare for deer and moose for five summer periods, and results of repeated measures analysis of variance in experiment B.

	Stand[a]						Stand		Time		Stand × time	
	1	2	3	4	5	6	$F_{[5,10]}$	P	$F_{[4,48]}$	P	$F_{[20,48]}$	P
Deer	ab	ab	a	bc	c	ab	4.61	**0.02**	1.21	0.32	0.73	0.77
1999	93.33 (35.28)	278.75 (53.29)	381.43 (103.62)	53.33 (17.64)	26.67 (26.67)	73.33 (6.67)						
2000	133.33 (17.64)	301.56 (76.16)	297.30 (78.47)	153.33 (65.66)	53.33 (43.72)	153.33 (46.67)						
2001	133.33 (13.33)	252.85 (95.72)	418.52 (154.8)	46.67 (46.67)	20.00 (11.55)	140.00 (80.83)						
2002	93.33 (43.72)	163.40 (1.71)	605.31 (116.02)	60.00 (30.55)	13.33 (13.33)	60.00 (50.33)						
2003	160.00 (50.33)	100.26 (33.32)	474.84 (147.76)	53.33 (24.04)	40.00 (23.09)	53.33 (6.67)						
Moose	ns	ns	ns	ns	ns	ns	2.16	0.14	1.64	0.18	0.29	1.00
1999	6.67 (6.67)	7.84 (7.84)	55.61 (28.48)	13.33 (6.67)	6.67 (6.67)	13.33 (6.67)						
2000	13.33 (6.67)	16.73 (8.42)	56.32 (26.64)	6.67 (6.67)	20.00 (20.00)	6.67 (6.67)						
2001	0.00 (0.00)	7.84 (7.84)	107.66 (55.09)	6.67 (6.67)	6.67 (6.67)	6.67 (6.67)						
2002	6.67 (6.67)	0.00 (0.00)	64.17 (42.85)	0.00 (0.00)	0.00 (0.00)	6.67 (6.67)						
2003	0.00 (0.00)	0.00 (0.00)	83.42 (42.73)	6.67 (6.67)	0.00 (0.00)	0.00 (0.00)						

Note: Columns of mean values with different letters are significantly different by Duncan's multiple range test, adjusted for multiple contrasts. ns, not significant.
[a]1, young plantation; 2, thinned (1000 stems/ha); 3, thinned (1000 stems/ha) and fertilized; 4, unthinned; 5, mature; 6, old-growth stand.

Table 6. Mean (n = 3 replicate stands; SE in parentheses) number of fecal pellet groups per hectare for deer and moose for four winter periods, and results of repeated measures analysis of variance in experiment B.

	Stand[a]						Stand		Time		Stand × time	
	1	2	3	4	5	6	$F_{[5,10]}$	P	$F_{[3,36]}$	P	$F_{[15,36]}$	P
Deer							3.16	0.06	3.40	**0.03**	0.53	0.91
1999–2000	100.00 (0.00)	165.00 (34.99)	335.10 (44.22)	100.00 (41.63)	40.00 (30.55)	400.00 (234.38)						
2000–2001	160.00 (64.29)	351.41 (91)	903.32 (217.44)	213.33 (6.67)	60.00 (34.64)	380.00 (160.42)						
2001–2002	113.33 (6.67)	368.15 (119.48)	1190.65 (146.23)	233.33 (83.53)	33.33 (17.64)	293.33 (137.76)						
2002–2003	206.67 (73.33)	627.16 (134.06)	806.38 (131.48)	213.33 (67.66)	60.00 (41.63)	340.00 (150.11)						
Moose							2.57	0.10	0.81	0.50	0.70	0.76
1999–2000	13.33 (13.33)	24.58 (13.63)	64.17 (22.67)	33.33 (17.64)	6.67 (6.67)	40.00 (20.00)						
2000–2001	20.00 (0.00)	31.37 (31.37)	52.05 (31.59)	26.67 (13.33)	13.33 (13.33)	6.67 (6.67)						
2001–2002	6.67 (6.67)	8.89 (8.89)	79.85 (22.17)	26.67 (13.33)	0.00 (0.00)	13.33 (6.67)						
2002–2003	26.67 (6.67)	0.00 (0.00)	31.37 (31.37)	33.33 (17.64)	0.00 (0.00)	20.00 (20.00)						

[a]1, young plantation; 2, thinned (1000 stems/ha); 3, thinned (1000 stems/ha) and fertilized; 4, unthinned; 5, mature; 6, old-growth stand.

Fig. 3. Mean (95% confidence interval) number of fecal pellet groups per hectare for mule deer in the six treatment stands during (*a*) summer (n = 15) and (*b*) winter (n = 12) periods at the replicate study areas from 1999 to 2003 (experiment B). Yg Plt, young plantation; Th, thinned; Th+F, thinned and fertilized; Unth, Unthinned; Mat F, Mature forest; Old G, old-growth forest.

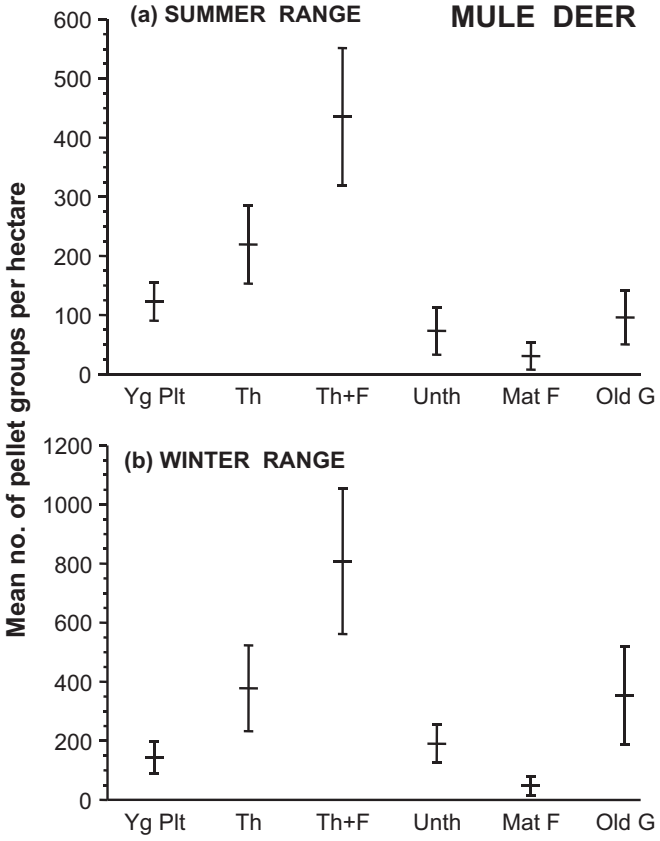
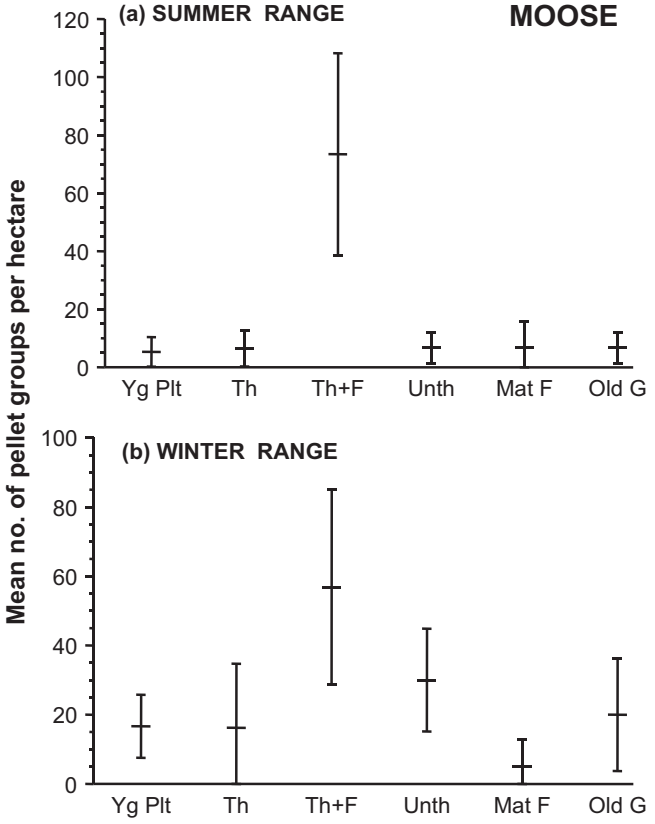


Fig. 4. Mean (95% confidence interval) number of fecal pellet groups per hectare for moose in the six treatment stands during (*a*) summer (n = 15) and (*b*) winter (n = 12) periods at the replicate study areas from 1999 to 2003 (experiment B). Yg Plt, young plantation; Th, Thinned; Th+F, thinned and fertilized; Unth, Unthinned; Mat F, mature forest; Old G, old-growth forest.



parison to mature and old-growth stands. During summer months, habitat use by deer was enhanced by PCT with repeated fertilization, and the 1000 stems/ha fertilized stands experienced greater use than the unthinned or mature stands. Winter habitat use by deer was unaffected by density or fertilization of young lodgepole pine stands. However, because the 1000 stems/ha fertilized stands had similar use levels as old-growth stands, and they were presumably superior to mature stands, this may be a major step towards creation of winter range for mule deer in young managed forests (Carey and Curtis 1996; Hayes et al. 1997).

In both summer and winter, moose preferred fertilized to unfertilized stands, and low-density to high-density stands. This result was similar to those of Ball et al. (2000) and Lavsund (1987) for moose and forestry interactions in Scandinavia. Browsing of coniferous and deciduous trees in fertilized plantations has been a particularly difficult problem in forests of Scandinavia and other northern European locations (Edenius 1993; Ball et al. 2000).

The relatively higher use by deer and moose of our fertilized stands was likely directly related to forage production and availability, at least during the 5 years of our study. This result was similar to that reported for summer diets of mule deer in lodgepole pine habitats in Utah, where early-successional habitats, managed and unmanaged, had higher forage consumption by deer than in older forests (Deschamp et al. 1979). The effects of quality and quantity of forage on survival, body condition, and reproduction of ungulates have been well established (Cook et al. 1998). Condition of spring forage may significantly limit fawn production and survival of deer (Peek et al. 2002). In addition, energy gained in summer coupled with energy lost in winter has the greatest impact on body condition of deer (Parker 1988). Thus, enhancing forage production in intensively managed forest stands may enhance body condition of ungulates prior to winter (and perhaps during winter as well, depending on shrub growth and relative snow depths). This strategy could significantly improve the chances of survival for deer and moose during severe winters (Hanley and McKendrick 1985; Parker 1988). Peek et al. (2002) concluded that declining mule deer populations in western North America were correlated with deteriorating forage conditions on ranges.

Thus, our hypothesis that large-scale stand thinning and repeated fertilization, 6–10 years after initiation of treatments, would enhance relative habitat use by deer and moose in both summer and winter, compared to that in mature and old-growth stands, is partially supported. Deer use of the fertilized 1000 stems/ha stands was similar to that in old-growth stands and higher than that in mature stands in both seasons. However, moose use of these habitats was similar, although there was a trend for greater use of the fertil-

ized 1000 stems/ha stands. We chose this particular set of managed young stands — precommercially thinned to 1000 stems/ha and precommercially thinned to 1000 stems/ha plus repeated fertilization — because they are typical of the stands that would likely be fertilized in silvicultural management of lodgepole pine.

Fecal pellet group counts

Fecal pellet group counts are widely used to estimate relative animal abundance and relative distribution among habitats, particularly for various species of ungulates (e.g., Marques et al. 2001; Campbell et al. 2004). In western North America, counts of pellet depositions are considered generally effective for comparing broad areas of use, particularly in representing habitat use during a seasonal period, such as summer and winter seasons over several years (Loft and Kie 1988; Edge and Marcum 1989). Pellet group counts have been used to estimate ungulate distribution relative to topographic factors (Edge and Marcum 1989) and to rank the relative use of habitats (Loft and Kie 1988), as done in our study. This approach assumes that there is a wide range of use in habitats, thereby allowing differentiation of high-, medium-, and low-use habitats at a coarse-grained level. We chose to conduct our experiments over a wide range of treatments to test the extremes (e.g., stands with a very low density of 250 stems/ha in experiment A and the repeatedly fertilized 1000 stems/ha stands in experiment B) of habitat features such as food and cover that likely play an important role during habitat selection by mule deer and moose.

There are several concerns about the reliability of pellet group counts. It is important to note that the relative deposition of pellet groups at any one plot or microhabitat may not have been indicative of the importance or relative use of that particular plot or part of the stand (Loft and Kie 1988; Edge and Marcum 1989). Defecation rates may increase with increasing forage intake and nutrient concentration (Smith 1964), as well as forage digestibility and succulence (Rodgers et al. 1958; Wallmo 1981). Thus, if succulence and digestibility of forage varied across habitats, as it certainly appeared to in our study, pellet group counts, and hence deer preference for our fertilized stands, may have been exaggerated. Similarly, defecation rates of deer appear to decline with age (Smith 1964), such that variable population demographics among habitats could bias inferences about habitat preference. We did not have any information on the relative age structure of individual deer and moose using our study areas. Finally, defecation rates of deer are generally lower in winter than in summer, and so comparisons across seasons are not recommended (Rogers 1987).

Harestad and Bunnell (1987) have raised concerns about decomposition rates of deer pellet groups in different habitats and periods. However, we counted only "new" pellet groups on cleared plots for both summer and winter seasons over the 5-year period. Thus, it is unlikely that sufficient decomposition of pellets would have occurred over these relatively short 5-month (summer) and 7-month (winter) periods.

Study limitations

A major limitation to our study was that we did not know the time of deposition of pellet groups during winter periods. For example, did most habitat use occur in the early winter before snow depths became unmanageable for ungulates? We do not have an answer to this question without using a series of snow-tracking transects at periodic intervals to determine relative use throughout the winter (D'Eon 2001). Thus, it is premature to assume that our winter pellet group counts represent "winter range".

Similarly, our results are limited to the Montane Spruce dm (dry, mild) biogeoclimatic subzone at elevations ranging from approximately 1200 to 1500 m elevation in moderate snowpack zones. Ideally, our study should have covered several years with variable snowpacks and used both pellet group counts and snow-tracking to determine which habitats constitute true winter range.

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