

RELATIVE SPATIAL DISTRIBUTIONS AND HABITAT USE PATTERNS OF SYMPATRIC MOOSE AND WHITE-TAILED DEER IN VOYAGEURS NATIONAL PARK, MINNESOTA

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ABSTRACT: We examined the distribution and home range characteristics of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) at Voyageurs National Park, Minnesota. Pellet count transects revealed low densities of moose and higher densities of white-tailed deer, and provided evidence of partial spatial segregation between moose and white-tailed deer possibly due to habitat heterogeneity. There was limited interspecific overlap in the relatively large annual home ranges of radio-collared moose and white-tailed deer. Both moose and white-tailed deer exhibited significant selection for spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) vegetation types at the home range scale. White-tailed deer significantly selected a 12-20 m canopy height over all others while moose significantly selected 5-11 m and 21-30 m canopy heights over the 12-20 m canopy height. Moose significantly selected open/discontinuous canopy cover and white-tailed deer selected both closed/continuous and open/discontinuous canopy covers over dispersed/sparse canopy cover. Differential habitat selection between moose and white-tailed deer at Voyageurs National Park might be related to the differences between these species' abilities to cope with a northern mid-continental climate. Spatial segregation between moose and white-tailed deer at Voyageurs National Park may allow moose to persist despite the presence of meningeal worm (*Parelaphostrongylus tenuis*) in white-tailed deer.

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Moose inhabit a circumpolar region of northern boreal forests dominated by spruce (*Picea* spp.), pine (*Pinus* spp.), and fir (*Abies* spp.). The range of moose in North America has expanded since 1955 (Peterson 1955) while numbers throughout the range increased from approximately 940,000 to 975,000 between 1960 and 1990 (Karns

1998). Moose numbers in Minnesota increased eight fold from approximately 1,500 animals in 1960 to 12,000 in 1990 (Karns 1998). Numbers of moose in northern Minnesota may have peaked prior to the 1990 estimates as moose abundance in adjacent Ontario started to decline in the mid-1980s (Thompson and Euler 1987). Moose at

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Voyageurs National Park (VNP), Minnesota, are at the southern periphery of the species' North American range and within a low density range between two high moose density ranges to the northeast and northwest (Fuller 1986). In the last 10 years, the northwestern moose population has dropped dramatically and now only numbers a few hundred animals (M. Lenarz, Minnesota Department of Natural Resources, personal communication). White-tailed deer (WTD) expanded their distribution into northern Minnesota around 1900 and were common in the area by the 1920s (Petraborg and Burcalow 1965). WTD densities in northeastern Minnesota were estimated at between 6 and 8/km² in the late 1930s (Olson 1938, Petraborg and Burcalow 1965).

Moose and WTD are sympatric across a relatively narrow band of North America, and the species' habitat use patterns within this band are not well understood. The two species are thought to have occurred sympatrically in the area that is now VNP at least since the early 1930s (Cole 1987, Gogan et al. 1997). Fluctuations in WTD numbers might be due to changes in habitat and changes in moose population levels have been attributed to changes in vegetative types and seral stages (Mech and Karns 1978, Cole 1987). Following the 1971 Little Sioux Fire in adjacent Superior National Forest, Minnesota, moose densities increased to five times their previous number (Neu et al. 1974, Peek et al. 1976). Both moose and WTD were found to consume similar browse after a fire in northern Minnesota (Irwin 1975). Active fire suppression within VNP has limited recent natural disturbances, and together with logging restrictions, affected the vegetation composition. The low frequency of wildland fires since the establishment of VNP could be a factor contributing to relatively low densities of moose. In the absence of specific information on moose and WTD distribu-

tions and habitat use patterns at VNP, the relationship of each species to vegetative conditions remains unclear.

Parasite mediated competition between moose and WTD might be responsible for recent declines in moose numbers. Meningeal worm, a parasite that is characteristically benign in WTD but fatal in moose, has been attributed for moose declines in Minnesota and elsewhere (Karns 1967, Prescott 1974). The extent to which meningeal worm impacts moose abundance at VNP is an unresolved issue. Spatial separation and differential habitat selection between moose and WTD may allow moose to persist in the presence of infected WTD (Gilbert 1974). WTD in Nova Scotia were excluded from some habitats at high elevation by snow depth, providing moose with refuges from WTD during the winter season (Telfer 1967). A "refugium" between moose and WTD in Ontario was identified as a possible factor allowing moose to persist in the presence of sympatric populations of meningeal worm-infected WTD (Kearney and Gilbert 1976). Questions however have been raised concerning the validity of the refugia hypothesis. The purported benefits of seasonal refugia for moose in warmer months when the potential infection rate is highest might not exist because moose and WTD habitat use overlapped during other times of the year (Nudds 1990). Even partial refugia from infected WTD however may provide moose with a relative advantage (Whitlaw and Lankester 1994).

In the absence of specific information on moose and WTD distributions and habitat use patterns at VNP, the relationship of the abundance of each species to vegetative conditions and the potential for moose refugia from meningeal worm infection remains unclear. This study was initiated to determine the relative spatial distribution and home range characteristics of moose and WTD at VNP, and to examine the

influence of habitat types on these distributions, and to assess overlapping use patterns of the two species.

STUDY AREA

VNP encompasses 882 km² on the southern portion of the Canadian Shield along the U.S.-Canada border. VNP is made up of a central landmass largely surrounded by lakes, called the Kabetogama Peninsula, and adjacent lands. Approximately 40% of VNP is covered by 4 large lakes. There is little overall elevation change with a maximum topographic relief of 80-90 m (Johnson and Sales 1995). Adjacent areas in Minnesota include lands administered by the state (Kabetogama State Forest), the federal government (Superior National Forest), and privately owned lands. Adjacent areas of Ontario are mainly Provincial Crown Lands. The study area boundary was defined as the area encompassed within the GIS vegetation coverage (USGS 2001) of the VNP region (Fig. 1).

Climate

The climate is characterized as cold winters and cool summers. Temperature extremes during the study period ranged from 35°C (August 1, 1989) to -39°C (December 30, 1990, National Weather Service, International Falls, MN). Average annual snowfall is 160 cm, with the most snowfall occurring during January (31 cm). The winter of 1988 – 1989 was a high snow year with 266 cm. Snowfall in the winter of 1989 – 1990 was 155 cm, close to the long-term mean, while snowfall in the winter 1991 – 1992 was 247 cm, considerably higher than the mean. The first significant winter snowfall usually occurs in early November, and the last significant snow usually occurs in early April (National Weather Service, International Falls, MN). The North Atlantic Oscillation (NAO) index (Lamb and Pepler 1987, Hurrell 1995) showed that winter temperatures were colder than average during the study period, with the winters of 1988 – 1989 and 1989 – 1990

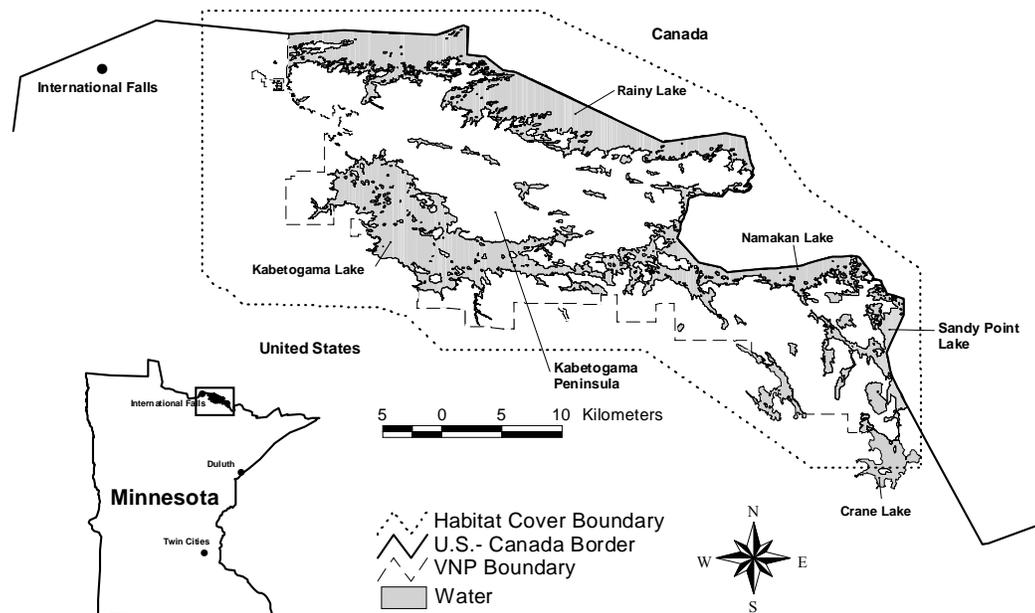


Fig. 1. Location of Voyageurs National Park, northern Minnesota.

being particularly cold.

Vegetation

VNP lies on the boundary between southern boreal forest and northern hardwood forest types (Pastor and Mladenoff 1992). Northern hardwood forests are dominated by red pine (*Pinus resinosa*), white pine (*P. strobus*), red maple (*Acer rubrum*), and black ash (*Fraxinus nigra*) (Kurmis et al. 1986). Southern boreal forest types are characterized by a mosaic of secondary growth jack pine (*P. banksiana*), white spruce (*Picea glauca*), quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) (Kurmis et al. 1986). The soil in the region is thin and sandy (Ohmann and Ream 1971).

Varying sources and levels of disturbance have created spatial heterogeneity in the vegetation of the VNP region. Logging has been an important influence on the current spatial distribution of vegetation across much of VNP. Parts of VNP, including approximately 25% of the Kabetogama Peninsula, were extensively logged between 1910 and 1930 (Crowley and Cole 1995). The combined impacts of these harvests decreased the abundances of white spruce, balsam fir, white pine, and red pine on the Kabetogama Peninsula. The relative abundance of aspen consequently increased to higher levels post-harvest. While logging practices within VNP ceased with the inception of the park in 1975, the majority of forested lands adjacent to the park have continued to be managed for timber harvest. Fire suppression efforts began in 1911 and have since limited major fires in the park region to 1917 – 1918, 1923, and 1936. Fires burned substantial portions of the Kabetogama Peninsula in 1923 and 1936, adding to the mosaic of vegetative cover in VNP (Fig. 2). Human and naturally caused wildfires within the

park since 1936 have been relatively small (<2.0 km²).

Wildlife

Woodland caribou (*Rangifer tarandus*) and moose are thought to have been the most common ungulates in the VNP region in pre-historic times (Cole 1987). WTD expanded northward into the region in the late 1890s and were reported to be common in the region by the 1920s (Petraborg and Burcalow 1965). Woodland caribou were extirpated from the region by the 1940s (Gogan et al. 1997). Moose possibly declined in numbers from the establishment of the park in the mid – 1970s through the mid – 1980s (Cole 1987). Approximately 60 – 100 moose were estimated to inhabit VNP at a mean density of 0.23/km² in the early 1990s (Whitlaw and Lankester 1994, Gogan et al. 1997). Estimated densities of WTD in and immediately adjacent to VNP ranged from 1.5/km² to 11.5/km² from 1975 (R. O. Peterson, Michigan Technological University, unpublished report, 1976) through 1992 (Whitlaw and Lankester 1994, Gogan et al. 1997). The reasons for the recent variations in moose and WTD population levels are unknown.

METHODS

GIS Vegetation Coverage

Habitat availability of the study area was determined using a Geographic Information System (GIS) vegetation coverage created by interpreting 1:15,840-scale color infrared (CIR) aerial photographs taken in 1995 and 1996 (USGS 2001). The entire coverage consisted of 156,886 ha, of which VNP comprised 88,244 ha (56%) of the total. A total of 40 vegetation cover types defined the ground features within the project area. Each vegetation cover type was further classified by canopy height and canopy density. For this study, we consolidated the original 40 GIS vegetation cover

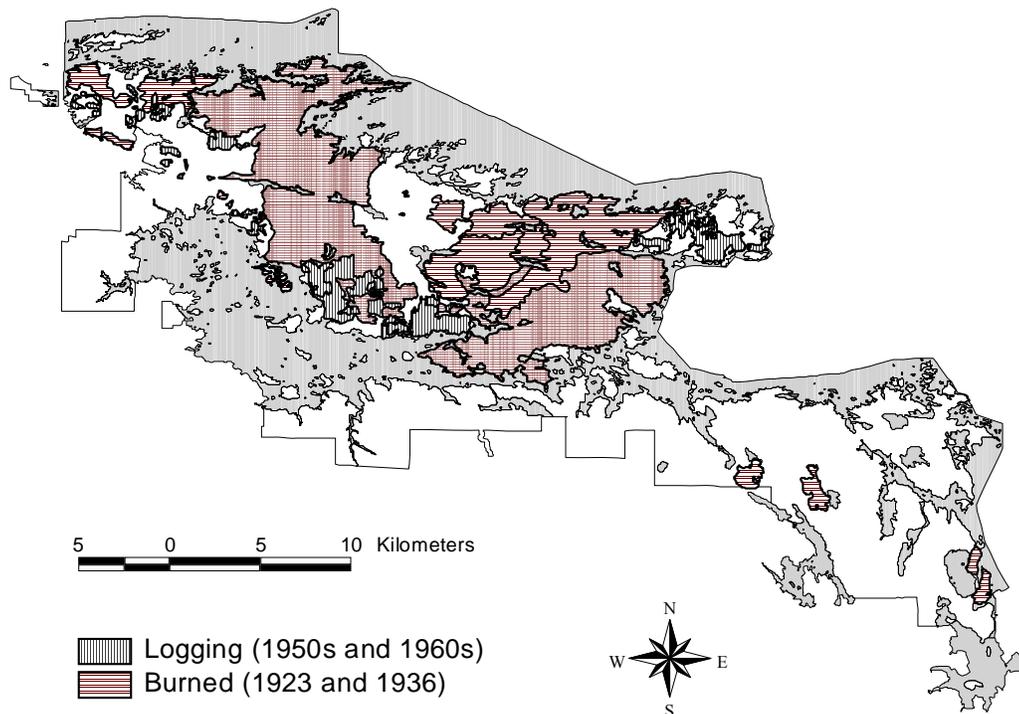


Fig. 2. Historical fire and logging locations within Voyageurs National Park, Minnesota.

types into 8 classes based on functional groups to facilitate analysis and alleviate the problem of missing habitat types during compositional analysis (Table 1).

Pellet Group Transects

We applied a 1 – km² grid to a 1:50,000-scale map of the park and randomly selected 32 cells as pellet group transect sampling units. Two parallel transect lines were established in a north-south orientation with at least 100 m separation between transect lines within most sampling units. Sampling units containing >50% water cover (11 of 32, or 34%) were limited to one transect line resulting in a total of 53 transect lines within the 32 sampling units. Each transect line was 800 m long and consisted of 4 plots (22 m by 3.6 m) at 200 m intervals. A survey chain (20 m) was used to measure distance traveled while surveying.

Transect lines were sampled once in late May of 1989 and again in the late May

of 1991, after snow melt and prior to the onset of new vegetative growth. All pellet groups within each plot above the previous fall's leaf litter were identified to species and tallied. We used the total number of moose and WTD pellet groups observed along each transect line in our analysis. We sampled 16 paired and 14 single transect lines in 1989, and 19 paired and 12 single lines in 1991. Some sampling units (4 of 32, or 12.5%) were only visited one year due to a lack of personnel and access problems (private land, terrain). To insure that the detection probability was even between sampling units containing 1 and 2 transect lines, we randomly selected a single transect line from sampling units containing 2 transect lines for analysis.

Numbers of moose and WTD pellet groups detected within each sampling unit by sampling year were entered into a GIS for interpretation. For moose, sampling units were stratified into those with pellet

Table 1. Description of vegetation classes used in compositional analysis. Consolidated vegetation classes were created by combining original GIS habitat classifications from the USGS/NPS vegetation coverage of the Voyageurs National Park region.

Consolidated Classes	Original GIS Habitat Classification	Consolidated Classes	Original GIS Habitat Classification			
Shrubland Alliance	Beaked Hazel/Serviceberry shrubland alliance	Bur Oak	Bur Oak/Oak (White, Northern Pin, Black) woodland alliance			
	Bog Birch/Willow saturated shrubland alliance		Bur Oak forest alliance			
	Leatherleaf saturated dwarf shrubland alliance		Aspen/Birch	Paper Birch forest alliance		
	Red Osier Dogwood/Willow seasonally flooded shrubland alliance			Quaking Aspen/Paper Birch forest alliance		
	Speckled Alder seasonally flooded shrubland alliance			Trembling Aspen temporarily flooded forest alliance		
	Northern White Cedar/Red Maple saturated forest alliance			Quaking Aspen woodland alliance		
	Northern White Cedar/Yellow Birch forest alliance			Herbaceous Alliance	Canada Bluejoint seasonally flooded herbaceous alliance	
	Northern White Cedar forest alliance				Cattail/Bulrush semipermanently flooded herbaceous alliance	
	Northern White Cedar saturated forest alliance				Common Reed semipermanently flooded herbaceous alliance	
	Tamarack saturated forest alliance				Few-seeded/Wiregrass Sedge saturated herbaceous alliance	
	Black Ash/Red Maple				Black Ash/Red Maple saturated forest alliance	Hardstem/Softstem Bulrush semipermanently flooded herbaceous alliance
					Jack Pine	Jack Pine/Lichen nonvascular alliance
			Jack Pine forest alliance			Mosaic/Complex (5 wetland herbaceous alliances)
Jack Pine, Red Pine woodland alliance	Mosaic/Complex (7 wetland herbaceous alliances)					
Red/White Pine	Red Pine forest alliance	Pondweed/Hornwort/Waterweed permanently flooded herbaceous alliance				
	White/Red Pine and Quaking Aspen forest alliance	Poverty Grass herbaceous alliance				
	White Pine forest alliance	Yellow/White Water Lily permanently flooded herbaceous alliance				
Spruce/Balsam Fir	Black Spruce/Quaking Aspen forest alliance AND/OR White Spruce/Balsam Fir/Aspen forest alliance	Wild Rice semipermanently flooded herbaceous alliance				
	Black Spruce forest alliance					
	Black Spruce saturated forest alliance					
	White Spruce/Balsam Fir forest alliance					

groups “present” and those without pellet groups “absent”. For WTD, sampling units were stratified on the basis of abundance into low (1–21 pellet groups) and high (>21–42 groups) use areas. We determined the average percent composition of vegetation types, canopy densities, and canopy heights for sampling units within each stratum of moose and WTD from the modified GIS vegetation map of VNP. We performed *t*-tests to examine differences between habitat proportions in absent vs. present stratum of moose sampling units and high vs. low stratum of WTD sampling units.

Capture and Radio Telemetry

We fitted 10 moose (3 bulls, 7 cows) with motion-sensing radio telemetry collars on the Kabetogama Peninsula between February 26 and March 2, 1989. Each moose was immobilized and sedated with a mixture of carfentanyl and xylazine hydrochloride via a barbed syringe fired from a helicopter. The immobilizing drugs were reversed with a hand injection of naltrexone. We fitted motion-sensing radio telemetry collars on 20 white-tailed deer (9 bucks, 11 does) within VNP between January 24 and March 9, 1989. Thirteen WTD were captured within the Moose Bay-Black Bay region, 5 along the Daley Brook snowmobile trail, and 2 on or adjacent to Cutover Island. WTD were captured in collapsible clover traps (Clover 1956) and immobilized using a pole-mounted syringe with a mixture of ketamine hydrochloride (Ketaset) and xylazine hydrochloride. The immobilizing drugs were reversed with an intravenous hand injection of talozoline. Instrumented moose and WTD were relocated via aerial radio telemetry at approximately 10-day intervals from January 24, 1989 to May 16, 1991. Relocations were attempted on all animals throughout the study period unless there was a mechanical failure in the radio collar or the animal was confirmed dead.

We calculated moose and WTD home ranges rather than use individual point relocations in habitat analyses to account for errors associated with radio telemetry point relocations (Kernohan et al. 1998). We created 90% adaptive kernel home ranges for individual moose and WTD using Home Range Extension (Rodgers and Carr 1998) in ArcView 3.2 (ESRI 2000). The data were standardized by dividing each value of *x* and *y* by its respective standard deviation (Seaman and Powell 1996). We calculated the smoothing factor (*h*) individually for each animal using the biased cross-validation (BCV) method (Sain et al. 1994).

We limited our calculation of annual home ranges to those animals for which we secured a minimum of 30 relocations since kernel home range estimates suffer from inaccuracies and inflated sizes when small numbers of animal locations are used (Seaman et al. 1999). All moose and 15 WTD were used in the home range analysis. One collared WTD fawn, approximately 9 months old at capture, was initially associated with a collared doe. This animal was included in the analysis because it established its own individual home range soon after capture, and therefore its locations were independent from its dam. We tested for significant differences between the mean sizes of moose and WTD home ranges and between male and female WTD mean home range sizes in VNP. Samples of male moose (*n* = 3) were inadequate to test for sexual differences in moose home range size.

Habitat Availability

We determined available habitats separately for moose and WTD as 2 extended 100% minimum convex polygons (MCP) containing either all moose or all white-tailed deer radio-telemetry locations within our study area (Fig. 3). We widened each MCP by 1.2 km for moose and 0.5 km for

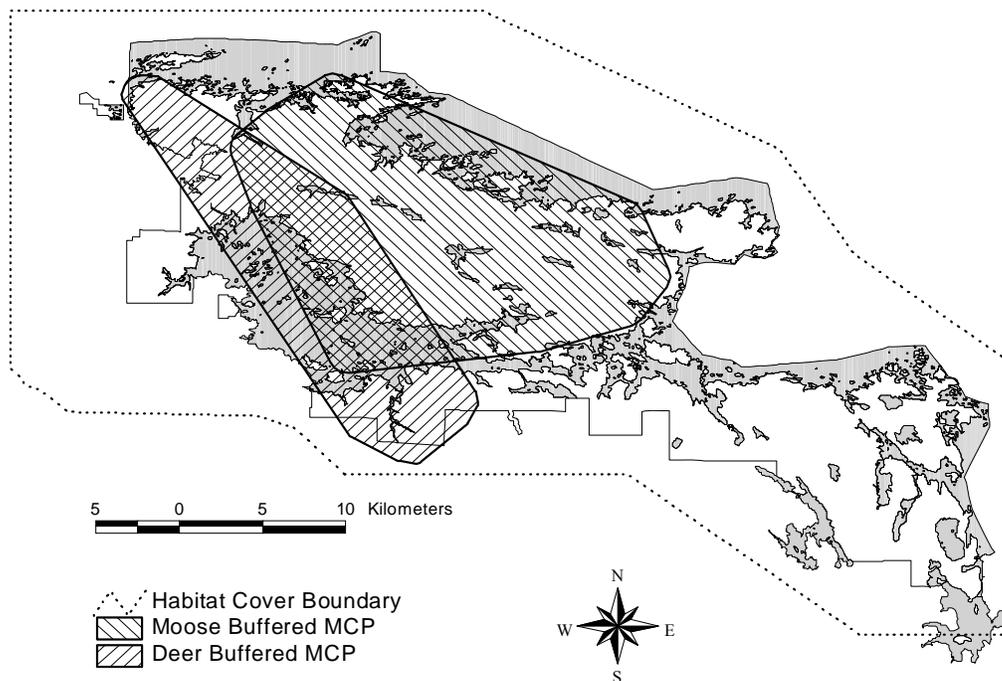


Fig. 3. Buffered minimum convex polygons of moose and WTD radiotelemetry locations, depicting areas used to delineate habitat availability for compositional analysis.

WTD to encompass the entire adaptive kernel home ranges of all study animals and calculated the percent composition of each habitat type available to moose and WTD using the extended MCPs. We clipped the modified GIS habitat coverage to individual moose and WTD adaptive kernel home ranges using ArcView 3.2 Patch Analyst extension (Rempel and Carr 2003). Lakes, ponds, and streams were excluded from habitat use or habitat selection calculations, however, vegetation adjacent to bodies of water were considered in the analysis. In addition to the 8 vegetation types, we examined the height and density of canopy covers within areas available to moose and WTD.

Habitat Selection

We compared habitat use to habitat availability using compositional analysis (Aebischer et al. 1993). Analysis was performed using the BYCOMP program

(Ott and Hovey 1997) within the SAS working environment (SAS Institute Inc. 2000). This program first determined whether habitat use differed from random using Wilks' Lambda (λ) statistics in multivariate analysis of variance (MANOVA). If habitat use was nonrandom, habitats were ranked in order of preference and levels of significance between ranks were determined using a *t*-test.

Only home ranges located entirely within the study area (GIS vegetation coverage extent) were included in habitat analyses. One migratory moose and one migratory WTD did not meet this criterion and were not used. Small sample sizes precluded seasonal and sexual habitat selection analysis. A minimum of 10 animals per group (season or sex) is needed to produce reliable results using compositional analysis (Aebischer et al. 1993). Our data would not have met these standards when partitioned into groups by season or sex. Compositional

analysis required that each animal use all habitat types (Aebischer et al. 1993). When proportional habitat use was estimated to be zero for moose and WTD, we replaced these values with 0.001. Substituting a value smaller than the smallest recorded nonzero value produced results that were robust relative to the substituted value (Aebischer et al. 1993).

RESULTS

Pellet Group Counts

A total of 1,674 deer pellet groups (820 in 1989, 854 in 1991) and 45 moose pellet groups (30 in 1989, 15 in 1991) were enumerated over all line transect surveys. WTD pellet groups were more abundant than moose pellet groups in all sampling units. Twenty-two of the 32 total sampling units (68.8%) contained no moose pellet groups. All sampling units contained WTD pellet groups at varying abundances ($\bar{x} = 16.8$, $SD = 12.0$).

Moose and WTD pellet groups occurrence varied spatially across VNP (Fig. 4). Moose pellet groups were present in low (0 - 13) abundances ($\bar{x} = 1.9$, $SD = 1.6$) in sampling units in the central and eastern regions of the Kabetogama Peninsula and absent from all other sampling units. WTD pellet groups occurred at high (>21 - 42 pellet groups) abundances in sampling units in the central and western regions of Kabetogama Peninsula and in the southeastern corner of the park, and low densities (0 - 20 pellet groups) in sampling units on the eastern end of the Kabetogama Peninsula. Only 3 sampling units (9.4%) contained moose pellet groups and high numbers of WTD pellet groups. These sampling units were located in the central region of the Kabetogama Peninsula and on the western periphery of moose pellet group distribution.

The abundance of moose and WTD pellet groups varied with the average per-

cent composition of sample unit habitat types. Sampling units with high abundances of WTD pellet groups contained significantly more spruce/balsam fir habitat than did sampling units with low abundances of WTD pellet groups ($t = 2.79$, $P = 0.02$, Table 2a). Sampling units with moose pellet groups contained significantly less closed/continuous canopy cover ($t = 2.25$, $P = 0.04$) and significantly more open/discontinuous ($t = 2.21$, $P = 0.04$) than did sampling units lacking moose pellet groups (Table 2b). Sampling units with moose pellets also contained significantly less 12 - 20 m canopy cover ($t = 2.37$, $P = 0.04$) than did sampling units lacking moose pellets (Table 2c).

Home Range

Moose and WTD were relocated by fixed-wing aircraft on a 10-day mean interval (min = 1, max = 119, $SD = 14$) for a period of 842 days. With outliers removed, 10 moose were relocated 786 times and 20 WTD were relocated 1,032 times. Each moose was relocated an average of 79 times (min = 30, max = 96, $SD = 22$). Each WTD was relocated an average of 52 times (min = 6, max = 76, $SD = 27$). Three (33%) radio-collared moose and 8 (40%) radio-collared WTD died during the study.

Moose home range averaged 48 km² (min = 29, max = 141, $SD = 33.5$). One male moose had an especially large home range of 141 km² because of seasonal migratory behavior. Excluding this animal, the average annual moose home range size was 37 km². The average annual WTD home range was 9 km² (min = 2, max = 49, $SD = 4.32$). One female WTD that exhibited seasonal migratory behavior had an especially large home range (49 km²). Excluding this animal, the average annual WTD home range was 6 km². The average moose home range was significantly larger than the average WTD home range ($t = 4.16$, $P < 0.01$, Fig. 5).

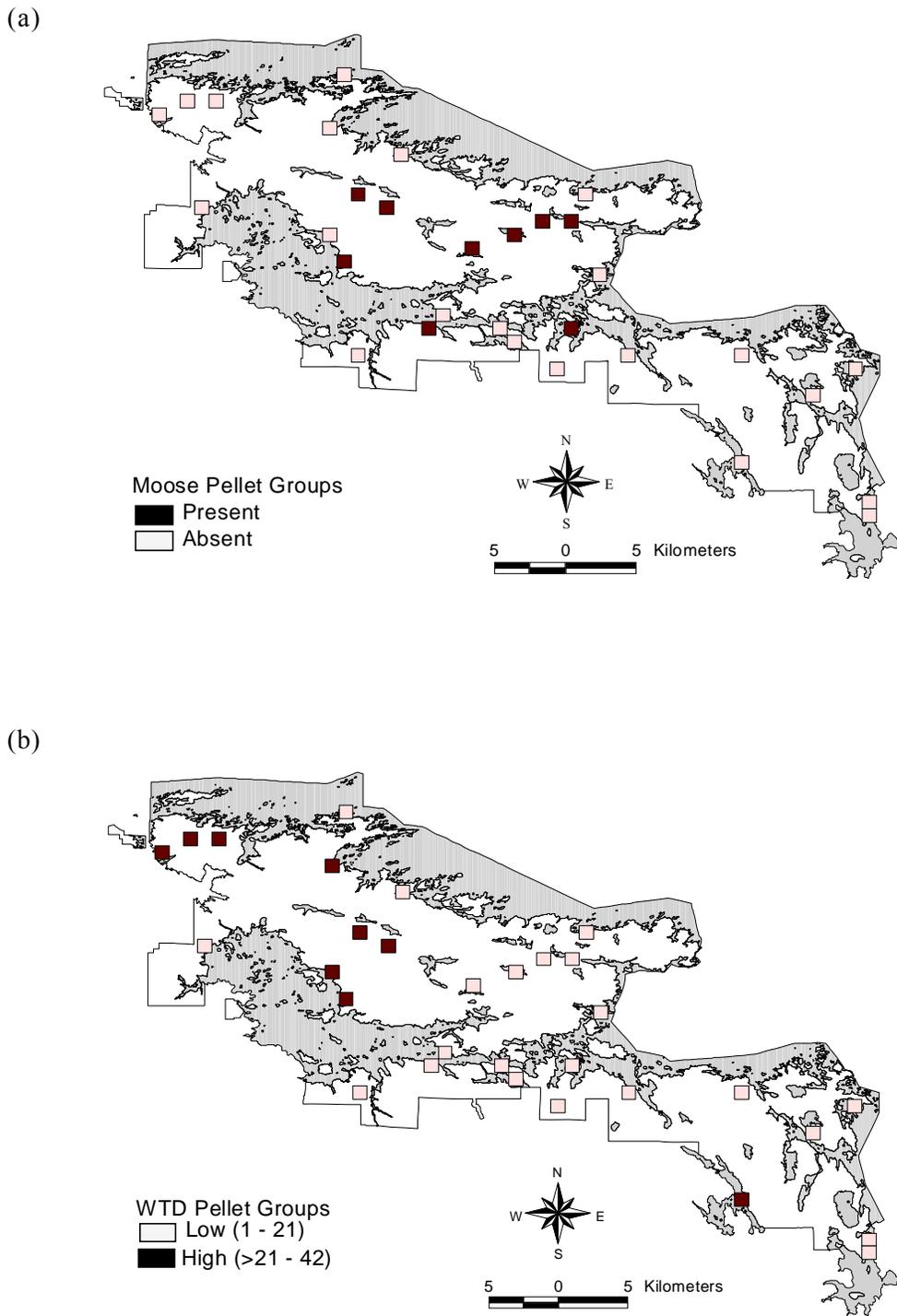


Fig. 4. (a) Presence or absence of moose pellet groups and (b) abundance of WTD pellet groups in sampling units at Voyageurs National Park, Minnesota, based on pellet count transects conducted in May 1989 and 1991.

Table 2. Percent composition of (a) vegetation types, (b) canopy densities, and (c) canopy heights found in moose sampling units that contained pellet groups (present) and that contained no pellets (absent), and white-tailed deer (WTD) sampling units that contained high (27-40) and low (0-12) abundances of pellet groups.

	Available	Moose		WTD	
		Present	Absent	High	Low
(a) Vegetation Type					
Aspen/Birch	23	23	25.4	20.1	26.7
Black Ash/Red Maple	2	2.7	1.2	2	1.4
Spruce/Balsam Fir	20.4	14.1	20	34.4*	12.0*
Bur Oak	8.9	19.1	4.9	6.1	9.6
Herbaceous Alliance	9.1	8	8.1	6.3	8.8
Jack Pine	15.5	11.9	20.8	12.8	20.9
Red/White Pine	17.6	15.8	17.5	16.5	17.3
Shrubland Alliance	3.5	5.4	2	2	3.3
(b) Canopy Density					
Dispersed/Sparse (10-25%)	0.4	0.4	0	0	0.6
Open/Discontinuous (25-60%)	27.1	41.2*	25.2*	28.3	29.7
Closed/Continuous (60-100%)	72.5	58.4*	74.8*	71.7	70.2
(c) Canopy Heights					
Open	9.3	7.7	8.3	5.9	9
<0.5 m	1.6	3.2	1.1	1.3	1.8
0.5 – 5 m	4.4	6.3	2.9	5	3.2
5 – 12 m	26.5	38.4	21	29.9	23.7
12 – 20 m	47.6	34.6*	55.6*	49.1	50.6
20 – 30 m	10.7	9.8	11.1	8.8	11.6

* indicates a significant difference ($\alpha = 0.05$).

The average male WTD home range (8 km²) was larger than the average female home range (4 km²), however, the difference was not statistically significant ($t = 0.30$, $P = 0.77$), even with the single female migratory WTD removed ($t = 1.33$, $P = 0.21$).

All WTD home ranges overlapped with

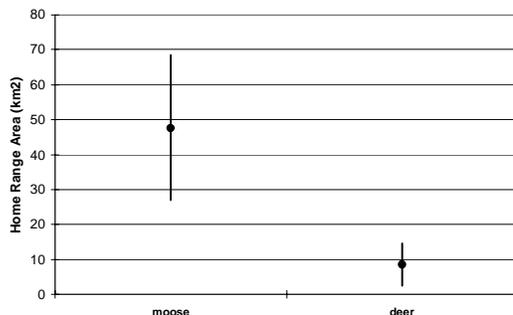


Fig. 5. Moose and WTD home range areas (km²), with 95% confidence intervals, at Voyageurs National Park, Minnesota.

at least one other WTD, and all moose home ranges overlapped with at least one other moose. Five of 10 moose home ranges overlapped with WTD home ranges, although the overlapping areas were relatively small. The total area of overlapping home ranges of instrumented moose and WTD was 6 km². This area of overlapping home ranges encompassed 2.5% of all moose home range area and 6.0% of all WTD home range area, and was located in the central Kabetogama Peninsula (Fig. 6).

Habitat Availability and Use

Available moose and WTD habitats were largely similar in terms of vegetation types, canopy height, and canopy density (Table 3). However, 58% of combined moose home ranges vs. 9% of WTD combined home ranges had been burned or

logged within the last 55 years.

Individual moose and WTD 90% kernel home ranges were largely similar in vegetation types with spruce/balsam fir and aspen/birch types making up $\geq 50\%$ of the vegetation type for both ungulates (Table 4). Jack pine was slightly more abundant than the herbaceous alliance in moose home ranges, whereas herbaceous alliance was the third most abundant vegetation type in WTD kernel home ranges. Moose and WTD showed similar rankings of abundance of canopy densities in their home ranges, however moose home ranges contained less closed/continuous and more open/discontinuous canopy densities than WTD. The 2 species differed in canopy height use with almost 50% of the 5 – 12 m height class available to moose and over 50% of the 12 – 20 m height class available to WTD.

Habitat Selection

Vegetation types within moose home ranges differed significantly from available

vegetation types ($\lambda=0.01$, $P=0.04$). Moose showed a significant preference for spruce/balsam fir over all other types except the shrubland alliance ($t = 2.12$, $P = 0.07$) and bur oak ($t = 2.22$, $P = 0.07$) (Table 5a). The shrubland alliance, aspen/birch, herbaceous alliance, bur oak, and red/white pine types all tied for second in preference and did not differ significantly in preference from one another. Moose exhibited significant nonrandom use of canopy densities ($\lambda=0.30$, $P = 0.02$). Moose significantly selected open/discontinuous canopy cover over all others, but exhibited no significant difference in preference between closed/continuous and dispersed/sparse canopies (Table 5b). Moose exhibited nonrandom use of canopy heights ($\lambda = 0.09$, $P = 0.03$) and showed a significant preference for 5 – 12 m canopy cover over open habitat and 12 – 20 m canopy cover (Table 5c). There was no significant difference in preference between 5 – 12 m and 20 – 30 m canopy height ($t=1.02$, $P=0.34$), or between 5 – 12 m and

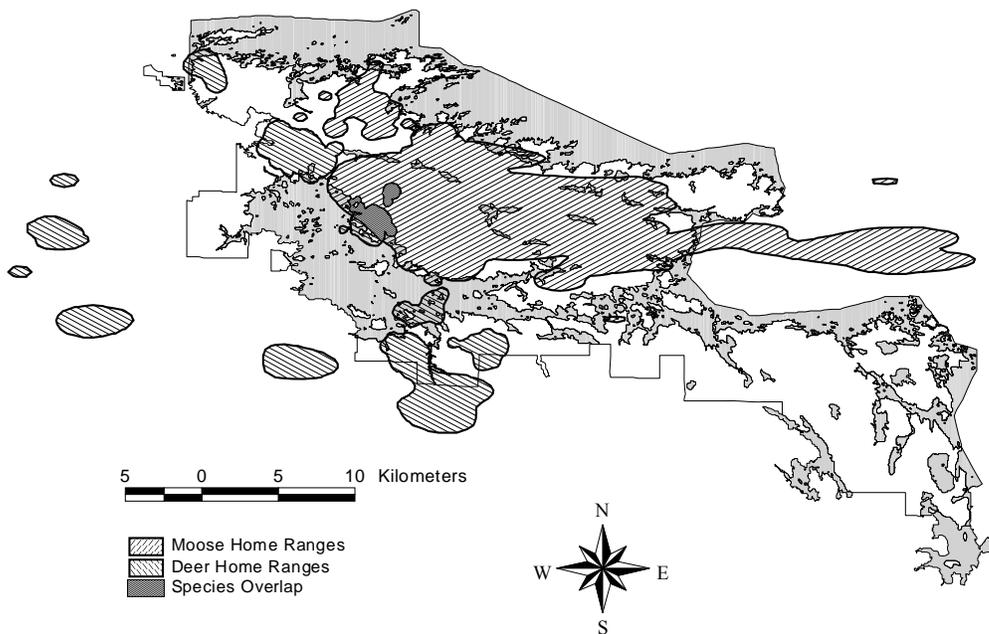


Fig. 6. Home range overlap of instrumented moose and WTD in and adjacent to Voyageurs National Park, Minnesota.

Table 3. Percent composition of available moose and white-tailed deer (WTD) (a) vegetation types, (b) canopy densities, and (c) canopy heights based on expanded minimum convex polygons of all moose and all WTD locations, respectively.

	Moose	WTD
(a) Vegetation Type		
Aspen/Birch	24.1	28
Black Ash/Red Maple	0.9	3.2
Spruce/Balsam Fir	26.8	26.6
Bur Oak	7.6	2.7
Herbaceous Alliance	11.2	13.3
Jack Pine	18.1	6.4
Red/White Pine	5.1	6.1
Shrubland Alliance	6.2	13.8
(b) Canopy Density		
Dispersed/Sparse (10-25%)	0.4	0.3
Open/Discontinuous (25-60%)	29.3	22.7
Closed/Continuous (60-100%)	70.3	77
(c) Canopy Heights		
Open	11.4	13.6
<0.5 m	2.2	2
0.5 – 5 m	6.3	9.8
5 – 12 m	34.3	33.1
12 – 20 m	44	39.3
20 – 30 m	1.8	2.1

0.5 – 5 m ($t = 2.39$, $P = 0.06$) or <0.5 m ($t = 2.25$, $P = 0.06$) canopy heights.

Vegetation types within WTD home ranges differed from available habitats but not significantly at P -value ≤ 0.05 ($\lambda = 0.25$, $P = 0.09$).

WTD significantly selected spruce/balsam fir over all other vegetation types except aspen/birch ($t = 2.03$, $P = 0.06$) (Table 6a). Aspen/birch was significantly selected over all remaining vegetation types except herbaceous alliance ($t = 1.83$, $P = 0.10$). Jack pine and bur oak tied for lowest in WTD preference at the home range scale. WTD exhibited significant nonrandom use of canopy densities ($\lambda = 0.27$, $P < 0.01$), significantly selecting closed/continuous

($t = 5.61$, $P < 0.01$) and open/discontinuous canopies ($t = 4.86$, $P < 0.01$) over dispersed/sparse canopy (Table 6b). Selection for closed/continuous canopy over open/discontinuous canopy was not significant at $P \leq 0.05$ ($t = 1.60$, $P = 0.12$). WTD exhibited nonrandom use of canopy heights ($\lambda = 0.11$, $P < 0.01$) with a highly significant ($P < 0.02$) preference for 12 – 20 m canopy over all others (Table 6c). There was no evidence of significant preference for any other canopy height.

DISCUSSION

Distribution

Pellet group sampling provided evidence that WTD were more widespread than moose at VNP. WTD pellet groups occurred in the high stratum toward the western and central portions of the Kabetogama Peninsula

Table 4. Average percentage habitat use within moose and white-tailed deer (WTD) 90% adaptive kernel home ranges.

	Moose	WTD
(a) Vegetation Type		
Aspen/Birch	22.6	28.2
Black Ash/Red Maple	0.5	2.5
Spruce/Balsam Fir	36.9	40.5
Bur Oak	7.2	2.1
Herbaceous Alliance	10	11
Jack Pine	11.6	3.1
Red/White Pine	4.4	5.5
Shrubland Alliance	6.8	7.3
(b) Canopy Density		
Dispersed/Sparse (10-25%)	0.3	0.1
Open/Discontinuous (25-60%)	37.4	20.4
Closed/Continuous (60-100%)	62.3	79.5
(c) Canopy Heights		
Open	10.1	11.1
<0.5 m	2.1	1.5
0.5 – 5 m	6.9	5.8
5 – 12 m	45.6	24
12 – 20 m	33.3	54.8
20 – 30 m	2.1	2.9

Table 5. Simplified ranking matrices for moose based on comparing proportional (a) vegetation type, (b) canopy density, and (c) canopy height use within 90% adaptive kernel home range to proportions available within the available area (extended MCPs). Habitat classes are ranked from most preferred to least preferred. Habitat classes that differ significantly in preference from random at $P = 0.05$ are indicated by either a “+++” or “—”. Habitat classes that differ in preference from random at $P = 0.10$ are indicated by either a “++” or “-”. Habitat classes that differ in preference from random at $P > 0.10$ are indicated by either a “+” or “-”.

	RANK	Spruce/Balsam Fir	Shrubland Alliance	Aspen/Birch	Herbaceous Alliance	Bur Oak	Red/White Pine	Jack Pine	Black Ash/Red Maple
(a) Vegetation Type									
Spruce/Balsam Fir	1	.	++	++	++	++	++	++	++
Shrubland Alliance	2	--	.	+	+	+	++	++	++
Aspen/Birch	3	--	.	.	+	+	+	++	++
Herbaceous Alliance	4	--	.	.	.	+	+	++	++
Bur Oak	5	--	+	+	++
Red/White Pine	6	--	--	++	++
Jack Pine	7	--	--	--	--	--	--	.	+
Black Ash/Red Maple	8	--	--	--	--	--	--	.	.
	RANK		Open/ Discontinuous (25-60%)		Closed/ Continuous (60-100%)		Dispersed/ Sparse (10-25%)		
(b) Canopy Density									
Open/Discontinuous (25-60%)	1		.		++		++		
Closed/Continuous (60-100%)	2		--		.		++		
Dispersed/Sparse (10-25%)	3		--		--		.		
	RANK	5-12 m	20-30 m	0.5-5 m	Open	<0.5 m	12-20 m		
(c) Canopy Heights									
5 – 12 m	1	.	+	++	++	++	++	++	++
20 – 30 m	2	.	.	+	+	+	++	++	++
0.5 – 5 m	3	--	.	.	+	+	+	+	+
Open	4	--	--	.	.	.	+	+	+
<0.5 m	5	--	--	+
12 – 20 m	6	--	--

and along the periphery of the southeastern portion of VNP while moose pellet groups were restricted to the central/eastern region of the Kabetogama Peninsula. The distribution of moose based upon our pellet group sampling and home range calculations were similar, and both agreed with the distribution of moose determined during aerial censuses (Gogan et al. 1997). The

capture and instrumenting of moose and WTD was completed prior to the establishment of the pellet group sampling transects and was therefore not dependent on our sampling of pellet groups. Our calculated home ranges of instrumented WTD were largely coincident with the distribution of pellet group units that we assigned to the high WTD stratum. Trapping locations for

WTD were based upon our observations of high concentrations of deer in winter and not on the distribution of high densities of pellet groups based upon our pellet group sampling in May.

While WTD pellet groups occurred in all sampling units, only 3 sampling units assigned to the high WTD stratum also contained moose pellet groups. This pattern is indicative of differing habitat use patterns between the 2 species. The inverse relationship between moose and white-tailed deer distributions at VNP is consistent with observations in adjacent Ontario, where moose reached their highest densities in areas where white-tailed deer were $\leq 4/\text{km}^2$ (Whitlaw and Lankester 1994). Moose densities in Ontario were inversely related to the mean intensity of meningeal worm larvae in white-tailed deer pellet groups (Whitlaw and Lankester 1994). There is currently no information on the relative spatial distribution of meningeal worm larvae in WTD pellet groups at VNP.

Home Range

Moose 90% adaptive kernel home ranges in VNP ($\bar{x} = 47.7 \text{ km}^2$, $n = 10$) were among the largest recorded in the contiguous United States, and were much larger than those found in northwestern Minnesota ($\bar{x}_{\text{male}} = 3.1 \text{ km}^2$, $\bar{x}_{\text{female}} = 3.6 \text{ km}^2$, $n = 26$) (Phillips et al. 1973) and northwestern Ontario ($\bar{x} = 14.0 \text{ km}^2$, $n = 1$) (Addison et al. 1980). The differences may be greater than these comparisons of size alone suggest since the other studies used methods that generally produce larger home range estimates than does the adaptive kernel method used here. Moose home ranges at VNP were substantially smaller than those in Alaska, where home range sizes (MCP) are between 120 km^2 and 350 km^2 (Gravogel 1984).

WTD adaptive kernel home ranges at VNP were larger than most recorded for

the species in the contiguous United States. Annual home ranges of WTD at VNP ($\bar{x} = 5.74 \text{ km}^2$, $n = 15$) were much larger than those in northeastern Minnesota (MCP, 0.8 km^2 summer, 0.4 km^2 winter) (Nelson and Mech 1981). In general, the home ranges of WTD at the northern limits of the species distribution are larger than those in the southern periphery of their range (Severinghaus and Cheatum 1956).

There are a number of causes for varying home range sizes between locations. Home range size might be dictated directly by an animal's energetics (McNab 1963). Following this theory, animals of the same species in more productive habitats have smaller home ranges than those in poor habitats, as the latter require greater areas to secure the resources required for survival. Other factors possibly influencing moose and WTD home range sizes at VNP include reproductive activity, relative distribution and diversity of suitable habitats, and species density (Leptich and Gilbert 1989, Beier and McCullough 1990, Ballard et al. 1991).

Sexual differences in home range size have been reported for moose and WTD. Males of both species usually occupy larger home ranges than females (Carlsen and Farnes 1957, Ballard et al. 1991) although no difference between male and female home range sizes has been observed in some areas (Phillips et al. 1973, Taylor and Ballard 1979, Hauge and Keith 1981). There was no significant difference between male and female WTD home range sizes at VNP. Our relatively small WTD sample caused large confidence intervals and strong outlier effects.

Moose and WTD in northern regions typically undergo significant seasonal home range shifts (Messier and Barrette 1985, Van Deelen et al. 1998). Yarding behavior by WTD is common in northern regions (Telfer 1967, Rongstad and Tester 1969,

Table 6. Simplified ranking matrices for white-tailed deer (WTD) based on comparing proportional (a) vegetation type, (b) canopy density, and (c) canopy height use within 90% adaptive kernel home range to proportions available within the available area (extended MCPs). Habitat classes are ranked from most preferred to least preferred. Habitat classes that differ significantly in preference from random at $P = 0.05$ are indicated by either a “+++” or “—”. Habitat classes that differ in preference from random at $P = 0.10$ are indicated by either a “++” or “-”. Habitat classes that differ in preference from random at $P > 0.10$ are indicated by either a “+” or “.”.

	RANK	Spruce/Balsam Fir	Aspen/Birch	Herbaceous Alliance	Black Ash/Red Maple	Shrubland Alliance	Red/White Pine	Jack Pine	Bur Oak
(a) Vegetation Type									
Spruce/Balsam Fir	1	.	++	+++	+++	+++	+++	+++	+++
Aspen/Birch	2	.	.	++	+++	+++	+++	+++	+++
Herbaceous Alliance	3	---	.	.	+	+++	+++	+++	+++
Black Ash/Red Maple	4	---	---	.	.	+++	+++	+++	+++
Shrubland Alliance	5	---	---	---	.	.	+	+	++
Red/White Pine	6	---	---	---	---	.	.	+	+
Jack Pine	7	---	---	---	---	.	.	.	+
Bur Oak	8	---	---	---	---
	RANK	Closed/ Continuous (60-100%)		Open/ Discontinuous (25-60%)	Dispersed/ Sparse (10-25%)				
(b) Canopy Density									
Closed/Continuous (60-100%)	1	.	.	+	.	.	.	+++	+++
Open/Discontinuous (25-60%)	2	+++	+++
Dispersed/Sparse (10-25%)	3	---	---	---	---	---	---	.	.
	RANK	12 – 20 m	Open	5 – 12 m	0.5 – 5 m	20 – 30 m	<0.5 m		
(c) Canopy Heights									
12 – 20 m	1	.	+++	+++	+++	+++	+++	+++	+++
Open	2	---	.	+	+	+	+	++	++
5 – 12 m	3	---	.	.	+	+	+	+	+
0.5 – 5 m	4	---	---	---	.	.	.	+	+
20 – 30 m	5	---	---	---	---	---	---	.	+
<0.5 m	6	---	---	---	---	---	---	.	.

Nelson 1998), and by moose in eastern Canada (Proulx 1983). Approximately 80% of white-tailed deer in nearby Superior National Forest, Minnesota, exhibit migratory behavior (Nelson 1998). Migratory behavior has traditionally been thought of as an adaptive response to the presence of

snow (Townsend and Smith 1933) or an anti-predator response (Nelson and Mech 1991). None of the WTD on the Kabetogama Peninsula exhibited migratory behavior typical of yarding based on the size and shape of their annual home ranges. One male moose extended its range into adjacent

Ontario in summer. Two white-tailed deer captured and radio marked in the vicinity of Daley Bay seasonally migrated during warmer months beyond the boundaries of the study area and returned to Daley Bay during the winter. Vegetation in the vicinity of Daley Bay is predominately northern white cedar swamp (classified as shrubland alliance in this study), which is typically associated with white-tailed deer wintering yards (Crawford 1982).

WTD may not exhibit migratory behavior in VNP because of an abundance of winter habitat. Forest maturation in adjacent Superior National Forest during the early 1970s provided white-tailed deer with abundant winter cover, and may have allowed the population to disperse into smaller groups rather than exhibit common yarding behavior (Wetzel et al. 1975). Winter cover, such as balsam fir, was abundant in VNP during this study due to a long-term absence of major wildfires and limited timber harvest in VNP since the 1930s, particularly in the area utilized by instrumented WTD. The potential abundance of preferred winter cover may be a reason for the non-migratory behavior of WTD at VNP.

There was minimal overlap between instrumented moose and white-tailed deer home ranges. Home range overlap between the two species was limited to a small region on the central Kabetogama Peninsula. Concurrent pellet group sampling showed the same region of the Kabetogama Peninsula to be the only area within VNP where moose pellet groups occurred within the high-density stratum for WTD pellet groups. Pellet group sampling showed that WTD occur throughout VNP at varying densities and that on the Kabetogama Peninsula, moose are generally limited to the central and eastern area.

Habitat Selection

Our pellet group surveys provided in-

formation on winter habitat use only, while the radio telemetry data provided information on the habitat characteristics of year-round home ranges. The pellet group surveys indicate that WTD preferred the spruce/balsam fir vegetation type over all others but did not select for canopy height or density. In contrast, moose showed no preference for any vegetation type but did prefer the open/discontinuous canopy densities, and avoided the dispersed/sparse canopy densities and 12 – 20 m canopy height. The year-round telemetry data reveal a different pattern with WTD and moose selecting for vegetative type, canopy density, and canopy height. We attribute this difference to differences in sampling intensity and portions of the annual cycle embraced by each sampling technique.

Moose distributions appeared to be related by the distribution of canopy heights and canopy densities in VNP. Lower canopy heights and canopy densities were more prevalent in sampling units containing moose pellets. The most common canopy height in sampling units containing moose was 5 – 12 m, but the most common canopy height in sampling units containing high abundances of white-tailed deer pellets was 12 – 20 m. Lower discontinuous vegetation might provide moose with more accessible forage in the winter.

Both moose and WTD at VNP exhibited a strong preference for spruce/balsam fir habitat types. This type satisfies different needs of each herbivore species. Moose habitat use generally is dictated by food abundance rather than shelter (Telfer 1970) and balsam fir is an important source of forage for moose in boreal forests, especially during the winter season (Irwin 1975, Peek et al. 1976, Ludewig and Bowyer 1985, Allen et al. 1987). However, balsam fir would also provide moose at VNP with a refuge from deep snow during winter: spruce and balsam fir were among the dominant

overstory species in moose winter yards in southern Quebec (Proulx 1983). WTD are less adapted to harsh winter conditions than moose and select winter habitat based on thermal protection and shelter, rather than forage preference (Telfer and Kelsall 1979). Spruce and balsam fir are considered poor quality forage for WTD (Crawford 1982, Blouch 1984) but offer WTD ideal winter protection. WTD in northeastern Minnesota used balsam fir dominated stands frequently in late winter (Wetzel et al. 1975). The unusually harsh winter conditions during our study might have caused white-tailed deer to utilize winter shelter habitats such as the spruce/balsam fir type for longer periods and at higher levels than usual. Monthly snowfall exceeded 50 cm in three consecutive months during the winters of 1988–1989 and 1990–1991, and remained into early spring following these winters. WTD movements become restricted at snow depths of approximately 30 cm and confined at snow depths ≥ 50 cm (Telfer 1970).

The aspen/birch vegetation type ranked second in WTD preference. Both species are preferred WTD forage in boreal forests (Cairns and Telfer 1980, Ludwig and Bowyer 1985). WTD in adjacent Ontario annually used aspen and birch more than other vegetation types (Kearney and Gilbert 1976). The aspen/birch type does not offer WTD as much thermal cover and snow protection as the spruce/balsam fir type.

The shrubland alliance, aspen/birch, and herbaceous alliance vegetation types all ranked second in moose preference. These types offer moose important forage species. Moose in northern Minnesota forage extensively on aspen and birch (Peek et al. 1976). The shrubland alliance includes northern red osier dogwood (*Cornus stolonifera*) and willows (*Salix* spp.) while the herbaceous alliance type contains hydrophilic plant species. Moose eat both the

woody and hydrophilic plants during the early spring and fall seasons in boreal forests (Peek et al. 1976, Jordan 1987). Aquatic habitats also may provide moose with an escape from biting insects during the early summer season (Ritcey and Verbeek 1969).

Moose and WTD selected different canopy densities and heights at VNP. Moose exhibited a significant preference for open/discontinuous canopy density to all other canopy densities and for canopy heights of 5–12 m and 20–30 m. WTD preferred closed/discontinuous canopy to open/discontinuous canopy densities and significantly preferred 12–20 m canopy height to all others. Differences between moose and WTD in body size may be an important factor in the differences in canopy preferences between these species. The amount of energy that ungulates expend in moving increases linearly with increasing snow depth, until breast height, at which it increases exponentially (Parker et al. 1984). Dense canopy cover displaces snow and causes structural changes to snow that influence the energy ungulates need to move and forage (Kirchoff and Schoen 1987). WTD are more restricted by snow depth and cold temperatures than are moose and therefore utilize vegetative types that allow movement during periods of deep snow (Telfer 1970). Moose are less affected by snow conditions than WTD and therefore would be more likely to select for forage availability rather than thermal and snow protection during winter. Moose winter yards in southern Quebec were in slightly closed canopy forest (41–80%) with tree heights of 9.1–18.3 m (Proulx 1983). However, these yards tended to be on slopes that reduced the energetic cost of moving through deep snow (Proulx 1983).

Moose selection of 20–30 m canopy cover was unexpected, however there are a few possible explanations for these observations. Low abundances of 20–30 m canopy

class were clustered throughout VNP, composed primarily of red/white pine overstory habitat. Although moose typically do not exhibit a high preference for white and red pine (Peek et al. 1976), as they did not in this study, understory vegetation in red/white pine habitat included aspen and birch that are palatable forage for moose. Heat stress avoidance is another possible explanation for moose selecting high canopy cover (Kelsall and Telfer 1974). Moose at VNP are at the southern periphery of the species' distribution. Southern populations of moose select forested upland sites during the summer season, possibly to reduce energy expenditure and enable them to forage for longer periods per day (Miller and Litvaitis 1992). During warm periods, the overhead canopy of a 20-30 m coniferous canopy could shade moose and reduce ambient temperatures better than other habitats.

Meningeal Worm Refuge

We did not find a single sampling unit that was free of WTD pellets. It is therefore highly unlikely that moose had a complete refuge from meningeal worm-infected WTD within VNP. Lower densities of WTD within moose range however might reduce the rate of meningeal worm transmission to moose, and thereby increase moose survival. This partial refuge could be enough to allow moose to survive in the presence of WTD. Moose are able to maintain low population levels in the presence of meningeal worm if WTD numbers do not exceed 4.6/km² (Karns 1967). Moose, WTD, and meningeal worm have existed sympatrically in Ontario since the early 1980s, and their interaction does not appear to be negatively affecting moose population numbers (Whitlaw and Lankester 1994). The prevalence of meningeal worm in WTD in northwestern Ontario was similar to VNP based upon the presence of larvae in feces and adults in the cranium

(Gogan et al. 1997).

Our pellet group surveys and radio telemetry data reveal evidence of spatial segregation and resource partitioning between moose and WTD at VNP. This spatial separation and differences in habitat preferences between moose and white-tailed deer at VNP may reduce the prevalence of meningeal worm infection in moose by providing moose with a partial refuge from meningeal worm-infected WTD (Gilbert 1974). The high prevalence of meningeal worm in WTD at VNP (Gogan et al. 1997) indicates that the parasite and its gastropod intermediate hosts are sufficiently abundant for transmission of the parasite to moose. The parasite is highly pathogenic to moose, and therefore moose are not expected to persist in its presence at VNP unless they are somehow isolated from infection. Moose densities in adjacent Ontario were lowest in areas with the highest mean intensity of meningeal worm larvae in WTD pellet groups (Whitlaw and Lankester 1994). The potential for meningeal worm transmission to moose may be even greater at VNP than Ontario since WTD densities and the prevalence of meningeal worm are higher at VNP than in most regions in Ontario (Whitlaw and Lankester 1994, Gogan et al. 1997). Partial habitat separation between moose and WTD at VNP may be a factor allowing moose to persist despite a high prevalence of meningeal worm.

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