ECOLOGICAL STATUS OF MOOSE AND WHITE-TAILED DEER AT VOYAGEURS NATIONAL PARK, MINNESOTA

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ABSTRACT: We examined the status and recent trends in numbers and distribution of moose and white-tailed deer along with prevalence of meningeal worm in both species at Voyageurs National Park, Minnesota. Aerial counts indicated deer occurred at a winter density of 8.37/km^2 throughout the park in 1992 while moose occurred at a density of 0.23/km^2 with a more limited distribution. Meningeal worm larvae occurred in 80% of the deer pellet groups examined in 1978 and 76% of the pellet groups examined in 1988 and 1989. Adult meningeal worms were found in 80% of the deer heads examined. A single dorsal-spined larva was recovered from 1 of 22 moose fecal samples. We conclude that white-tailed deer and moose have occured sympatrically at VNP through at least the 1980s. There is no direct evidence that meningeal worm is a mortality factor in adult moose at the park.

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The local extirpation of woodland caribou (*Rangifer tarandus*) in the first half of this century and reported declines in the abundance of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) in to the early 1980s (Cole 1987) shortly after the establishment of Voyageurs National Park (VNP) in 1975 prompted the National Park Service to initiate studies on the status of moose and white-tailed deer in 1987. The studies were intended to determine the effects of potential limiting factors on these sympatric ungulate species.

Moose have persisted at low densities in the park throughout the 1980s in the presence of a high density deer population. We report on the sympatry of moose and white-tailed deer and the prevalence of meningeal worm (*Parelaphostrongylus tenuis*) (Anderson and Prestwood 1981, Lankester 1987) at VNP between 1977 and 1992. We also review available information on wolf (*Canis lupus*) and black bear (*Ursus americanus*) predation in limiting moose numbers (Boutin 1992, Messier 1991, 1994).

STUDY AREA

VNP covers an area of 882 km^2 atop the Canadian Shield along a 50 km portion of the United States-Canada boundary between northern Minnesota and northwestern Ontario. The park's western boundary lies 20 km east of the communities of International Falls, Minnesota, and Fort Frances, Ontario. Large lakes separate the park's Kabetogama Peninsula and adjacent islands (329 km^2) from a southeastern land mass (206 km^2) (Fig. 1). Maximum topographic relief is 80 to 90 meters. Vegetation is a mixture of a western extension of the Great Lakes-St. Lawrence Forest and the northernmost range of the Minnesota-Wisconsin mixed forest (Sims *et al.* 1989). Forest cover is predominantly a mosaic of quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), jack pine (*Pinus banksiana*), and balsam fir

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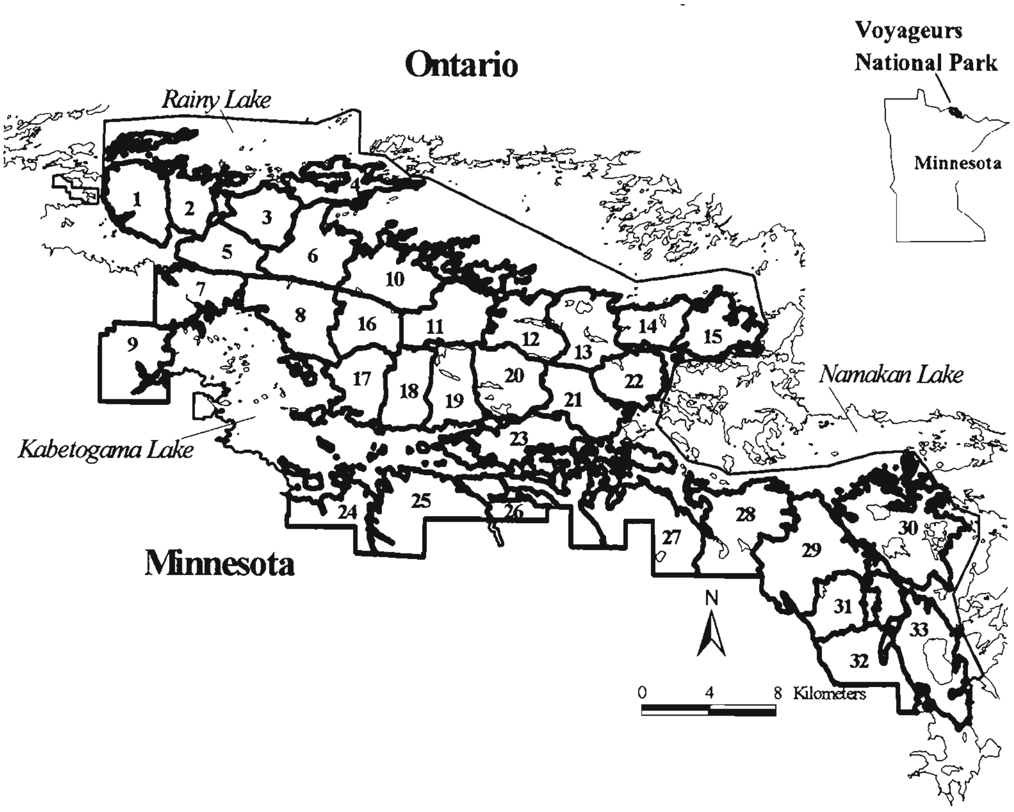

Fig. 1. Location of Voyageurs National Park, Minnesota, and distribution of survey units used for stratification of moose density and aerial censuses of moose and white-tailed deer, winters 1991 and 1992.

(*Abies balsamea*) (Kurmis *et al.* 1986). Forest canopy cover is approximately 80% in summer and 40-50% in winter (N. S. Duncan, unpublished data). Limited logging occurred in the 1930s. Subsequent to forest fires in the 1930s, wildfires were suppressed until the late 1980s when the National Park Service implemented a wildland fire management plan (National Park Service 1989).

VNP lies within the peripheral moose range for northern Minnesota, northwest of the state's northeastern primary range (Karns *et al.* 1974, Fuller 1986). The density of moose in Minnesota's peripheral range in the mid 1970s was estimated at < 0.12/km^2 while maximum density in the northeast primary range was estimated up to 1.4/km^2 (Karns *et al.* 1974). Silvicultural practices in the northeastern primary range are designed to favor moose (Forest Service 1986). Density estimates of moose in portions of northwestern Ontario adjacent to VNP ranged between 0.16 and 0.35/km^2 in 1992 (Whitlaw and Lankester 1994).

The range of white-tailed deer in Minnesota expanded northward after 1900 and the species was common in northeastern Minnesota by the 1920s (Petraborg and Burcalow 1965). Densities in northeastern Minnesota were estimated at between 6 and 8/km^2 from 1935 to 1939 (Olson 1938, Petraborg and Burcalow 1965). Deer wintered at high densities in the Shoepack Lake Area of the Kabetogama Peninsula in the mid-1950s (L. T. Magnus, Deer Yard Inspection Form, Minnesota Dept. of Conservation 1954). Densities of deer wintering southeast of VNP near the communities of Ely and Isabella, Minnesota, declined from 3.5/km^2 in the late 1960s (Mech and Karns 1977) to 0.75/km^2 by the winter of 1975-76 and to about 0.5/km^2 from the late 1970s through the early 1980s (Nelson and Mech 1986). Density increased to about 1/km^2 in the mid-1980s (Nelson and Mech 1986). The extent to which these shifts in density were mirrored in the area incorporated in to VNP remains unknown. Deer densities in VNP during the winter of 1975-76 varied from 1.5/km^2 to 11.5/km^2 (Peterson 1976). Silviculture practices on those portions of Superior National Forest immediately south of VNP are designed to favor white-tailed deer (Forest Service 1986) and density estimates ranged from 7 to 11/km^2 to 11/km^2 from 1979 to 1989 (M. Lenarz, MN Dept. of Natural Resources, Grand Rapids, MN, pers. comm.). Density estimates of white-tailed deer in portions of northwestern Ontario adjacent to VNP ranged between 2.5 and 5.7/km^2 in 1992 (Whitlaw and Lankester 1994).

METHODS

Numbers and Distribution

Moose numbers and distribution within VNP were determined annually by park staff from 1982 to 1987, in 1989, 1991 and 1992 using aerial strip counts. North - south flight lines or strips were spaced 0.8 km apart over the park's entire land mass and flown in a tandem 2-seater Piper PA 18 Super-Cub or tandem 2-seater Christen Husky at approximately 150 km/hr. The locations of all moose and moose tracks detected were recorded. Group size was recorded for all sightings of moose.

During the winters of 1991 and 1992, we utilized Gasaway *et al.*'s (1986) aerial block counts methodology to estimate moose density. In winter 1992, we explored the feasibility of counting white-tailed deer concurrently with moose and estimating population densities of both species using Gasaway *et al.*'s (1986) model. The land mass of VNP was divided into 31 survey units ranging in size from 13 to 24.5 km^2 (Fig. 1). Each survey unit was subdivided into approximately halves using topographic features and a half randomly selected for intensive searching. Thus, the areas selected for intensive sampling ranged in size from 7 to 13 km^2. This is a larger area for intensive survey than the 5 km^2 suggested by Gasaway *et al.* (1986) but reflects the low density of moose anticipated throughout the sample area. In 1991 and 1992, survey units were stratified relative to moose density from the "strip counts." Those survey units in which any moose or >2 groups of moose tracks were observed were assigned to a low density strata. All others were assigned to a no moose stratum. Survey units were not stratified for deer.

Survey units were sampled by circling to maximize use of contours and topography. Average air speed during the counts was between 100 and 130 km/hr. Average altitude was 200 m above ground level. The entire survey unit was sampled initially at a search rate of 3.5 minutes/km^2. Both the observer and pilot searched the area from the side of the aircraft oriented toward the ground at any moment. Once detected, animals were circled to determine group size and to plot group location. Upon completion of the initial search, the randomly pre-selected subunit of each area was resampled with a search effort of approximately 5 minutes/km^2. The pilot was not aware of which portion of the survey unit was to be sampled more intensively until after the initial survey had been completed. Again, group size and location of animals sighted were plotted and recorded. The observer and pilot determined whether or not each group detected had been sighted on the initial survey. Adjacent survey units were sampled as closely in time as possible to reduce any confounding effects due to animals moving between survey units. All data were analyzed with program MOOSEPOP (Gasaway *et al.* 1986). Key to the program's subroutine for estimating density is developing a sightability correction factor (SCF_0) based upon the ratio of animals detected in the initial and intensive sampling of the survey units.

The winter distribution of moose in 1991 and 1992 was determined from the locations of moose detected from the aerial strip and survey unit counts. The winter distribution of deer was determined from sightings during the aerial survey counts in 1992.

Meningeal Worm

Deer fecal samples were collected throughout VNP from 26 January to 21 March 1988 (n=41) and from 10 January to 26 March 1989 (n=56). We recalculated the incidence of meningeal worm larvae in deer fecal samples at VNP using only those samples Rowe (1978) collected between January and February 1978 (n=104). These periods were selected to reduce the likelihood that samples were contaminated with soil-dwelling nematodes or that larvae had been lost by the action of melting snow and spring rain (Peterson and Lankester 1991).

We collected the heads of deer dying of natural causes within the park between 1 January and 5 March 1988 (n=12) and from 12 October 1988 to 9 April 1989 (n=48). Deer were classified as fawns (<1 yr), yearlings (≥1 and <2 yr) and adult (≥2 yr) by patterns of eruption, replacement and wear on the teeth (Severinghaus 1949). Age estimates of both dead and live-captured adults were refined by counting cementum annuli on incisor or canine teeth (Gilbert 1966, Ransom 1966).

The intact heads of 2 female radio-collared moose were recovered subsequent to their deaths in December 1989 and April 1990, respectively. Moose fecal samples were collected off snow throughout VNP from 10 January to 20 March, 1989 (n=13) and from the colons of 9 of 10 (3 male, 7 female) moose immobilized and radio-collared between 26 February and 2 March, 1989. The age of 7 of the 10 radio-collared moose was determined by counting cementum annuli of canine teeth secured at the time of capture or death (Sergeant and Pimlott 1959, Gasaway *et al.* 1978).

All fecal samples and heads of both deer and moose were frozen soon after collection. With the exception of 2 moose heads, samples were transported frozen to the Minnesota Department of Natural Resources' Forest Wildlife and Populations Research Group, Grand Rapids, MN, for analysis. The prevalence of meningeal worm in fecal samples of moose and white-tailed deer was determined by the standard Baermann technique for 24 h. A control set of fecal samples from captive white-tailed deer known to be infected with meningeal worm was analyzed simultaneously to confirm the efficacy of the technique (pers. comm. K. Kerr, MN Department of Natural Resources, Grand Rapids, MN). Heads of deer were examined by removing the soft tissue and bone to expose the dura mater. The dura mater and dorsal surface of the cerebrum were examined for the presence of adult brain worm prior to removing the brain. The remainder of the brain and the cranial cavity were inspected subsequent to removal of the brain. The cavernous sinus was also inspected (pers. comm. K. Kerr, MN Department of Natural Resources, Grand Rapids, MN). Two intact moose heads were transported frozen to Lakehead University and examined for evidence of brain worm following the same general protocol by M. W. Lankester (pers. comm. M. W. Lankester, Lakehead University, Thunder Bay, Ontario).

RESULTS

Numbers and Distribution

A low of 23 and maximum of 47 moose were detected in seven annual aerial strip counts over the entire park land mass (Fig. 2) completed between 1980 and 1992, generating density estimates ranging between 0.04/km^2 in both 1980 and 1989 and a peak of 0.09/km^2 in 1986. The high density estimate in 1986 corresponds with a calf:adult ratio of 57:100, the highest recorded at VNP (Fig. 2). Calf:adult ratios in all other years are less than half the level observed in 1986. A calf:adult ratio of 9:100 was recorded during aerial counts of the survey units on the Kabetogama Peninsula portion of the park in 1991 and 1992.

We flew strip counts on February 2-3 1991 to stratify the survey units. Seventeen survey units (304 km^2) were classified as low moose density while the remaining 14 (231 km^2) were assigned to the no moose stratum. The unavailability of an aircraft prevented conducting the block counts until March 11. The census was terminated due to warm temperatures and insufficient snow cover on March 14 after only 6 (109 km^2) of 17 low density survey units had been sampled. All 6 survey units were on the Kabetogama Peninsula. Nineteen moose were seen on the initial counts and an additional 4 moose were seen in the intensive counts resulting in a mean density estimate of 0.28/km^2 and a 90% CI estimate of between 23 and 57 moose in the area sampled (Table 1).

We flew strip counts over the park on January 31 and February 1, 1992. Ten survey units (205 km^2) were classified as low moose density while 21 (338 km^2) were assigned to the no moose stratum. All survey units assigned to the low density stratum were on the Kabetogama Peninsula. These 10 survey units were sampled between February 9 and March 3. Twenty-eight moose were tallied during the initial counts. All moose detected on the initial counts plus 7 not seen initially were sighted during the intensive searches of the randomly selected segments of these survey units. The resulting density estimate is 0.23/km^2 with a 90% confidence interval

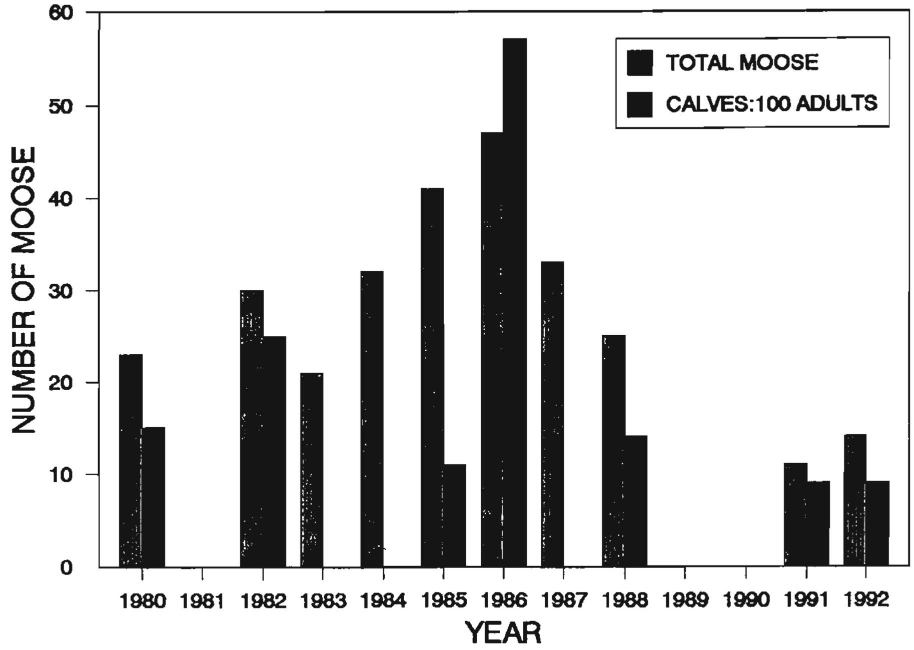

Fig. 2. Numbers and adult:calf ratios of moose detected during aerial strip counts of Voyageurs National Park, Minnesota, between 1980 and 1992.

Table 1. Calculated sightability correction factors (SCF$_0$) and resulting estimate of density per km2 and numbers of moose in 1991 and 1992 and deer in 1992 on select portions of the Kabetogama Peninsula, Voyageurs National Park, Minnesota.

Species	Year	Area (km^2)	SCF$_0$	Density	90% CI	Numbers	90% CI
Moose	1991	109	1.60	0.28	0.0-0.52	22	23[a] - 57
Moose	1992	205	1.70	0.23	0.12-0.35	49	35[a] - 72
Deer	1992	329	2.25	2.94	1.79-4.09	967	664[a] - 1345

[a] Lower range of confidence interval is truncated at the number of animals actually seen during the aerial counts.

estimate of between 35 and 72 moose in that portion of the Kabetogama Peninsula assigned to the low moose stratum (Table 1). Moose were widespread throughout VNP in 1991 but detected on the Kabetogama Peninsula only in 1992 (Fig. 3). Nearest-neighbor analyses of the locations of moose groups detected during the 1984-86 strip counts and the 1991-92 strip and block counts provide an index of aggregation of 2.0 and 1.78, respectively, indicative of a regular distribution of moose groups (Krebs 1989:128).

White-tailed deer were detected and counted in all 19 survey units on the Kabetogama Peninsula between February 4 and March 12, 1992. A total of 474 deer was tallied in the initial surveys of which 129 were in the segments of the survey units randomly pre-selected for intensive sampling. The intensive sampling resulted in a tally of 304 deer in all of these randomly pre-selected segments. The resulting mean density estimate is 2.94/km^2 for the Kabetogama Peninsula (Table 1).

Meningeal Worm

The prevalence of meningeal worm in deer pellet groups in 1978 was 80%. The pooled prevalence in the winters of 1987-88 and 1988-89 was 76%, with the values in 1987-88 being higher than in 1988-89 (Fig. 5). There is no significant difference in prevalence between these years ($\chi^2=2.19$, df=2, P=0.33).

The prevalence of meningeal worm in aged deer carcasses pooled for 1987-88 and 1988-89 was highest in yearlings (Fig. 5). Prevalence was 80% in adults. Ages of adult deer ranged from 3 to 15 years. Meningeal worm larvae were isolated from 1 of the 13 moose fecal samples collected off of snow and none of the 9 fecal samples collected from immobilized moose. Neither of the 2 heads examined showed any sign of infection with meningeal worm (pers. comm. M. Lankester, Lakehead University, Thunder Bay, Ontario). The immobilized moose ranged in age from 2 to 10 years.

DISCUSSION

The aerial strip counts reveal that moose occurred at low numbers in VNP throughout the 1980s and in to the early 1990s. Estimates of moose density derived from the strip counts are questionable as the method is seriously flawed for the following reasons: 1) the strips provided incomplete coverage of the park; 2) since no measurement was made of the distance from the aircraft that moose were detected, it is not possible to calculate the area of the park actually sampled; and 3) the aircraft deviated from its flight line to follow fresh tracks of moose, resulting in an estimate of density biased by the unknown probability of encountering fresh moose tracks. Such problems with strip counts have been recognized for a considerable period of time and alternate sampling methods pro-

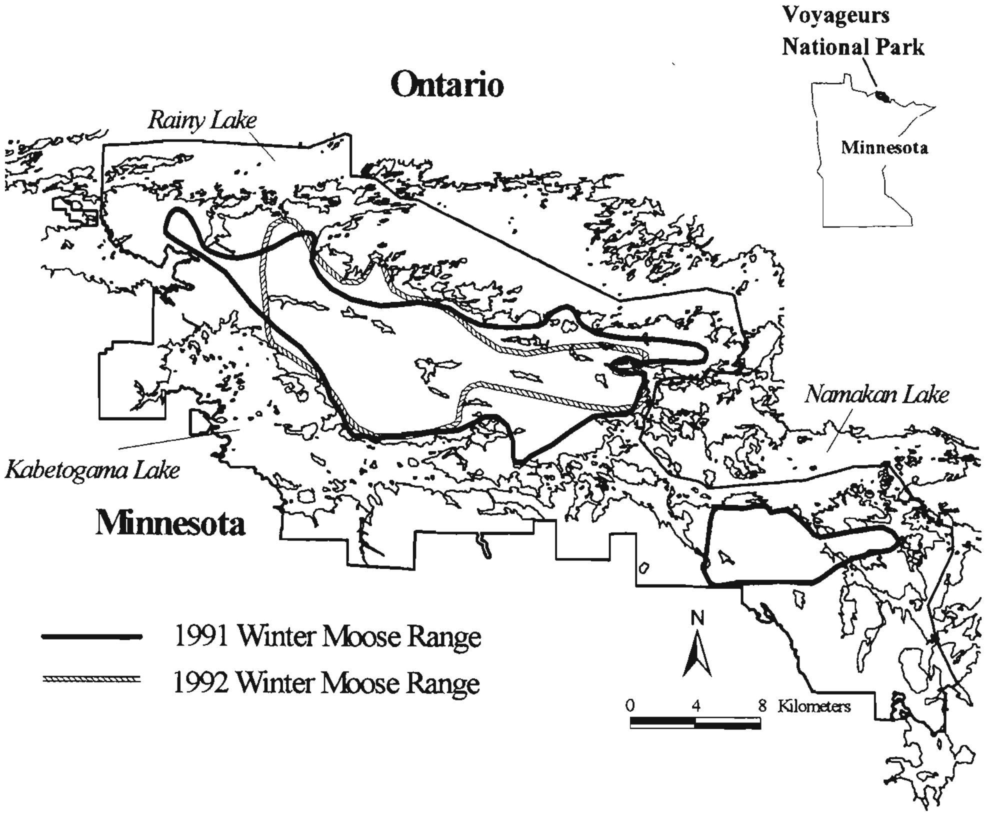

Fig. 3. Winter distribution of moose at Voyageurs National Park, Minnesota, for 1991 and 1992 determined by aerial surveys.

posed (Gasaway *et al.* 1986, Rivest *et al.* 1990).

Similarly, previous efforts to determine white-tailed deer densities in the park have produced less than satisfactory results. An effort to estimate deer density throughout the park by an aerial census of 18 randomly selected 1.3 km^2 plots was inconclusive but indicated winter densities varied from 1.5/km^2 to 11.5/km^2 (Peterson 1976). We consider an estimated deer density of 1.5/km^2 parkwide derived from the same strip counts used to census moose (Cole 1987) as suspiciously low for the reasons mentioned above.

The optimal time for aerial counts of moose in the Great Lakes region is as early in winter as adequate snow cover permits (normally December) (Lynch 1975, Peek *et al.* 1976, Crête *et al.* 1986, Peterson and Page 1993). Thus, the February - March counts of moose at VNP in 1991 and 1992 were done under less than optimal conditions. This was related to lack of availability of an aircraft in both years. The SCF_0 of 1.6 for the abbreviated moose count in 1991 and 1.7 for the more extensive moose count of 1992 indicates that no more than 60% of the moose present were detected in the initial searches of the survey units. We believe that these values are a minimum estimate of animals missed. Both SCF_0 estimates are higher than values reported for 4 moose counts in interior Alaska (Gasaway *et al.* 1986) but lower than detection levels for midwinter censuses of moose at Isle Royale National Park (IRNP), Michigan, where 75% of the moose present

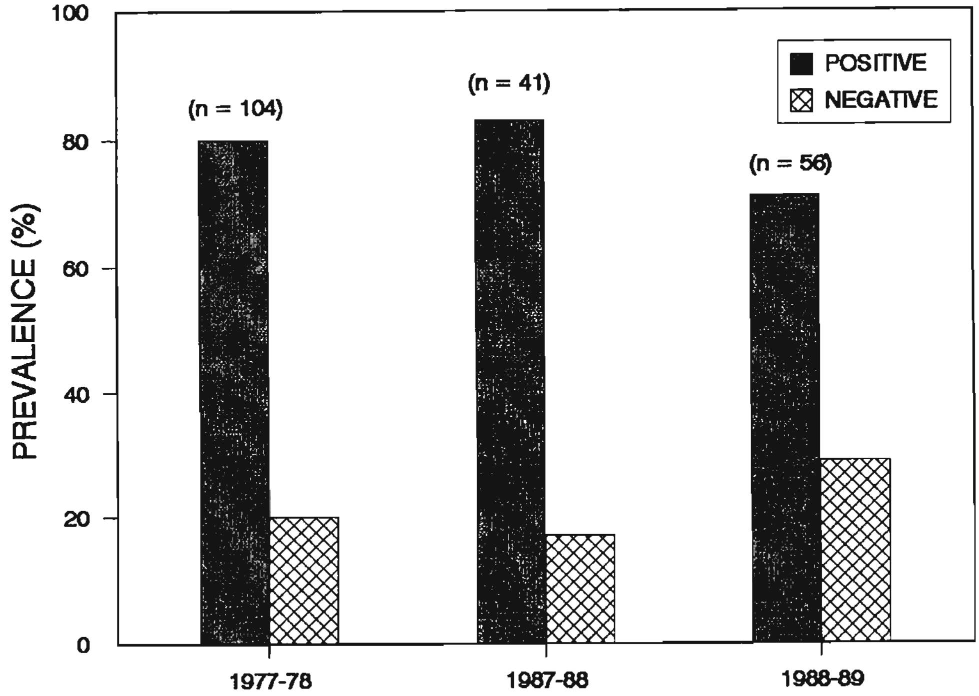

Fig. 4. Prevalence of meningeal worm larvae in white-tailed deer pellet groups collected during the winters of 1977-78, 1987-88, and 1988-89 at Voyageurs National Park, Minnesota.

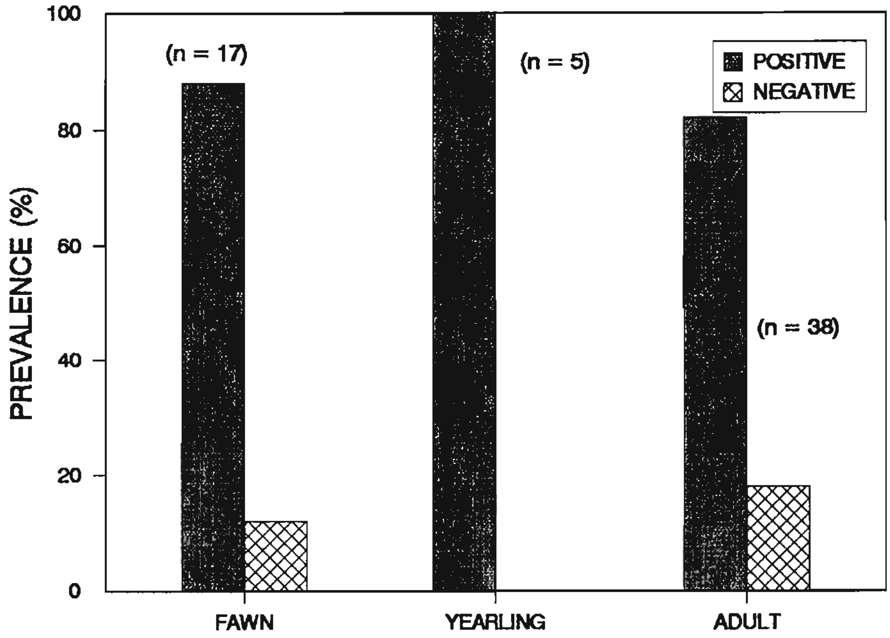

Fig. 5. Prevalence of meningeal worm adults in white-tailed deer heads collected during the winters of 1987-88 and 1988-89 at Voyageurs National Park, Minnesota.

are assumed to be detected (Peterson and Page 1993). Securing estimates of the proportion of animals detected by use of instrumented elk (*Cervus elaphus*) Samuel *et al.* (1987) reported detecting only 35% of the elk present during helicopter block counts in areas of closed canopy forest in Idaho.

The point estimates of a moose density of 0.28/km^2 and 0.23/km^2 for 1991 and 1992, respectively, (Table 1) suggests that application of of Gasaway *et al.*'s (1986) methodology to determine moose densities may provide consistent and reliable estimates over time. The close agreement in mean density estimates of moose between years (Table 1) is attributable in part to the fact that there is considerable overlap between years in the areas assigned to the low moose stratum. Both censuses centered upon the distribution of moose on the Kabetogama Peninsula. These density estimates for the low density moose strata at VNP are consistent with other estimates for low density strata in northeastern Minnesota of between 0.21 and 0.41/km^2 (Peek *et al.* 1976) and at IRNP, Michigan, of from 0.25 to 0.50/km^2 (Peterson 1977).

Their smaller size and lighter coloration render white-tailed deer more difficult to detect from the air than moose. We consider sightings during the survey flights too unreliable to permit stratification of deer distribution. Thus, all survey units were assigned to a single stratum. The greater difficulty in detecting white-tailed deer is reflected in the higher SCF_0 value for deer in 1992 than the comparable values for moose in both years (Table 1). The SCF_0 value for deer may be an underestimate as there were occasions when deer groups sighted on the initial counts were not detected during intensive sampling. Such occurrences will reduce the estimate for the SCF_0. The calculated SCF_0 values for deer in 1992 (Table 1) indicate that 45% of the deer detected during the more intensive sampling were detected on the initial surveys.

Other aerial censuses of white-tailed deer in northern Minnesota have derived a sightability estimate by comparing the number of radio-collared deer detected during aerial censuses to the number subsequently determined to be present in the census area. This is comparable to the sightability correction factor SCF_0 of Gasaway *et al.* (1986:31). Long-term estimates of sightability of deer in the Ely and Isabella deer yards suggest that as few as 35% of the deer are actually seen, resulting in a SCF_0 of 2.85 (pers. comm. M. E. Nelson, Biological Resources Division - USGS, Ely, MN). Application of this SCF_0 to our 1992 mean density estimate of white-tailed deer on the Kabetogama Peninsula of 2.94/km^2 (Table 1) increases our estimated density to 8.37/km^2 or 3,037 deer. Such an estimate falls within the range of deer densities of 7-11/km^2 south of VNP estimated by pellet group counts and population modelling (M. Lenarz, MN Dept. of Natural Resources, Grand Rapids, MN, pers. commun.). We suggest that 8.37/km^2 is a reasonable estimate of white-tailed deer density on the Kabetogama Peninsula portion of the park. The approximately threefold adjustment in estimated deer density reflects the difficulty in detecting deer from fixed-wing aircraft.

The prevalence of meningeal worm in deer at VNP was high during the latter part of the 1970s and 1980s (Fig. 4). Comparison of the prevalence of larvae in feces between locations requires caution. Prevalence rates in fawns is lower than in older age classes and varies by the season of collection (Peterson and Lankester 1991, Slomke *et al.* 1995). Seasonal differences are not signifigant in older age classes. Thus, overall prevalence levels may be influenced by the proportion of fawns in the population. Within the fawn age class, prevalence rates are higher in spring (March through May) than winter (December through February) or fall (September through November) (Peterson and Lankester 1991, Slomke *et al.* 1995). Our sampling of the prevalence of meningeal worm in feces from January through March covers two of these seasons. In two of our three sample years, prevalence levels at VNP are higher than a pooled prevalence level in deer from Grand Marais, Minnesota for winters 1986-87 through 1988-89 (Peterson and Lankester 1991) and 1991-92 and 1992-93 (Slomke *et al.* 1995) as well as portions of Ontario immediately north of VNP during winter (January through March) 1992 (Whitlaw and Lankester 1994).

The prevalence of adult meningeal worm in the heads of fawns is influenced by season and is lower than for other age classes (Slomke *et al.* 1995). There is no seasonal effect of the prevalence of meningeal worm in the heads of deer >1 year-old (Slomke *et al.* 1995). At VNP, the prevalence in heads for 1987-88 and 1988-89 (Fig. 5) confirms the prevalence detected in pellet groups (Fig. 4). Prevalence levels for fawns at VNP are higher than the highest seasonal level for fawns at Grand Marais, Minnesota, for 1991 through 1993 (Slomke *et al.* 1995). The prevalence levels in deer >1 year-old at VNP and Grand Marais, Minnesota, (Slomke *et al.* 1995) are comparable. Both are lower than the prevalence level in deer near St. Paul, Minnesota (Slomke *et al.* 1995). Similar regional differences have been reported for northern New York where prevalence levels varied by townships from 14% to 88% (Garner and Porter 1991).

The probability of white-tailed deer becoming infected with meningeal worm may be higher in deer yards in early spring and in those deer remaining in deer yards throughout the summer (Peterson and Lankester 1991, Lankester and Peterson 1996). Eighteen of 20 female white-tailed deer captured and radio-collared at VNP in January/February 1989 and radio-tracked through January 1992 were year-round residents of limited areas (Gogan, unpubl. data). Thus, non-migratory deer at VNP may be expected to exhibit a high prevalence of infection.

Lankester (1987) emphasized that prevalence data for meningeal worm reflects the overall success of the parasite in reaching its final host under prevailing conditions. Thus, the prevalence of meningeal worm in a deer herd has been interpreted as the best measure of the risk of sympatric moose being infected with the parasite. The number of deer shedding meningeal worm larvae has been reported as highest in spring in northeastern Minnesota (Peterson and Lankester 1991, Slomke *et al.* 1995) and Algonquin Provincial Park, southeastern Ontario (Anderson 1963). If deer at VNP shed fewer meningeal worm larvae in winter as do those at Grand Marais, Minnesota, then the prevalence levels determined by our winter sampling of pellet groups are an underestimate of the risk of sympatric moose being infected by the parasite.

More recently, the mean intensity (number of larvae per gram of infected fecal material) of meningeal worm larvae has been proposed as a more reliable indicator of the risk of transmission to moose (Whitlaw and Lankester 1994). We did not determine the mean intensity for the deer pellet group samples from VNP. However, the mean intensity of meningeal worm in deer fecal samples in winter 1992 in areas of Ontario immediately adjacent to VNP range from 10.8 to 34.9 larvae/g (Whitlaw and Lankester 1994). The latter value is one of the highest reported for northwestern Ontario and is coincident with moose densities of below 0.2/km^2 (Whitlaw and Lankester 1994).

The recovery of meningeal worm larvae from 1 of 22 moose fecal samples from VNP contrasts with the recovery of meningeal worm larvae from only 2 of 617 moose fecal samples collected from hunter kills throughout northern Minnesota in 1987 (pers. comm. M. S. Lenarz, MN Department of Natural Resources, Grand Rapids, MN) and from only 2 of 361 moose pellet group samples examined from northeastern Minnesota in

1965 (Karns 1977). The prevalence of meningeal worm in sympatric white-tailed deer in 1965 was 41% (Karns 1977). Upshall *et al.* (1987) detected no meningeal worm larvae in moose pellet groups in New Brunswick when the prevalence of larvae in pellet groups of sympatric white-tailed deer was 49%. These cases contrast with a reported meningeal worm larval prevalence of 9.6% for moose pellet groups in northern Maine when the prevalence level in sympatric white-tailed deer was 50% (Clark and Bowyer 1987).

The absence of meningeal worm in the 2 adult female moose heads is unremarkable. Radio tracking of both at approximately 10-day intervals prior to death revealed no indications of the neurological disorders characteristic of meningeal worm infection. Both moose died within their home ranges. Moose with characteristic signs of meningeal worm have been reported within 16 km of VNP's western and southern boundaries (pers. comm. J. Schneewies, MN Department of Natural Resources, International Falls, MN). Fuller (1986) reported recovering meningeal worm from 1 of 9 moose brains in an area of northcentral Minnesota with an 81% prevalence of meningeal worm larvae in deer pellets. In the Canadian maritime provinces, the parasite was been isolated from 80% of 45 moose exhibiting symptoms of the disease but only 5% of 115 moose not demonstrating symptoms (Smith and Archibald 1967).

Our record of the decade-long persistence of moose at low densities in the presence of white-tailed deer at higher densities is consistent with observations across much of northwestern Ontario (Whitlaw and Lankester 1994). While moose densities are comparable to the range of densities for northwestern Ontario, deer densities at VNP are higher than the range reported for northwestern Ontario (Whitlaw and Lankester 1994). Long-term coexistence of moose and deer, with deer at densities of 9-10/km^2 have been reported for select portions of Ontario (Whitlaw and Lankester 1994). However, moose densities across Ontario are highest where deer densities are <4/km^2 (Whitlaw and Lankester 1994). Such relationships may not be expected to continue indefinitely. The relative abundance of each species has flip-flopped in two of Ontario's provincial parks (Whitlaw and Lankester 1994).

It has been hypothesized that moose are able to persist in sympatry with white-tailed deer infected with meningeal worm by utilizing refugia in which deer are absent (Gilbert 1974). The validity of this hypothesis has been questioned (Nudds 1990). We believe that it is highly unlikely that any deer-free refugia exist within VNP for the following reasons: 1) deer were sighted in all aerial survey units during both 1991 and 1992, 2) deer pellet groups were detected on all of 50 sample plots randomly distributed throughout VNP in May of 1989 and 1991 (Gogan unpubl. data), and 3) deer occurred within the home ranges of all of 10 radio-collared moose between 1989 and 1991 (Gogan unpubl. data).

Modelling of moose - deer - meningeal worm interactions suggests that even in the absence of refugia a stable equilibrium between moose and deer characterized by moose less abundant than deer may develop, "when there is a high transmission rate of parasites to definitive hosts, a low parasite induced mortality rate, and a strong competitive difference between the definitive hosts" (Schmitz and Nudds 1994:97). The data for VNP demonstrate that there is a high transmission rate of meningeal worm to the normal definitive host and circumstantial evidence suggests that there is a low mortality rate in adult moose: 4 of 10 >2 year-old moose immobilized and radio-collared on the Kabetogama Peninsula during winter 1989 (Gogan unpubl. data) died prior to the winter 1995. The 6 survivors were re-instrumented during winter 1995 (pers. commun. J. Pastor, Univ. of Minnesota, Duluth). One of the surviving 6 moose died in November 1995 (pers. comm. J. Pastor, Univ. of Minnesota, Duluth). The parasite is considered to be almost benign in white-tailed deer (Anderson and Prestwood 1981, Lankester 1987). We have no information on the level of competition between moose and deer at VNP.

Our data are inadequate to provide a rigorous evaluation of either the refugia theory (Gilbert 1974) or the non-refugia model proposed by Schmitz and Nudds (1994). However, the data do suggest that models of moose - white-tailed deer - meningeal worm sympatry that do not include refugia warrant further investigation. Modelling of moose - wolf interactions as a single ungulate prey - predator system led Messier (1994) to conclude that wolf predation coupled with moose calf mortality induced by poor habitat or bear predation would result in moose coming in to an equilibrium at a density range of 0.2 - 0.4/km^2 (Messier 1994). The abundance of white-tailed deer, a prey species generally more vulnerable than moose to wolf predation, may either dilute the effect of wolf predation on moose through a functional response or exacerbate the impact of wolf predation on moose population dynamics through a numeric response (Messier 1994). Wolves occurred at a density of approximately 0.05/km^2 in the region of VNP between 1987 and 1991 (Gogan unpubl. data). White-tailed deer and beaver (*Castor canadensis*) constitute the main prey items in the diet of wolves in the region of VNP with moose hair detected in scats in March, April and July only (Schmidt 1990). Wolves remove 6 - 20% of the moose each year at moose population densities of 0.2/km^2 (Boutin 1992). At this predation rate, wolves would be predicted to kill between 3 and 10 of the approximately 50 moose on the Kabetogama Peninsula of VNP. Black bear densities in Superior National Forest of 0.16 - 0.24/km^2 (Rogers 1987) approach the level at which they may become a significant source or mortality on moose calves (Ballard 1992).

We conclude that white-tailed deer and moose have occured sympatrically at VNP through at least the 1980s. Both species were widespread and deer were more abundant than moose in the late 1980s and early 1990s. Our data is inadequate to identify specific factors limiting moose numbers in VNP.

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