ECOLOGY OF MENINGEAL WORM, *PARELAPHOSTRONGYLUS TENUIS* (NEMATODA), IN WHITE-TAILED DEER AND TERRESTRIAL GASTROPODS OF MICHIGAN'S UPPER PENINSULA WITH IMPLICATIONS FOR MOOSE

Pamela J. Nankervis[1,4], W. M. Samuel[1], Stephen M. Schmitt[2], and James G. Sikarskie[3]

[1]Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E9; [2]Michigan Department of Natural Resources, 8562 E. Stoll Road, East Lansing, MI 48823, USA; [3]Michigan State University, Veterinary Medical Center, A-226, East Lansing, MI 48824, USA

ABSTRACT: Moose (*Alces alces*) were reintroduced to Michigan's Upper Peninsula in the mid-1980's. Because some of the subsequent mortalities were attributed to meningeal worm, *Parelaphostrongylus tenuis*, a study was done in 1995 - 1996 to determine potential exposure of moose to this parasite. Objectives were to determine parasite population size in white-tailed deer (*Odocoileus virginianus*) of the region as well as the abundance and distribution of gastropod intermediate hosts with emphasis on their role in transmission of *P. tenuis* to moose. Sixty-nine of 158 (44%) white-tailed deer were infected with adult worms and 68 of 9,477 (0.7%) terrestrial gastropods were infected with larvae of *P. tenuis*. Prevalence and intensity of adult worms were lower in fawns (28%, all with 1 worm) than in older deer (51%, $\bar{x} = 1.7$). Numbers of first-stage larvae were more numerous in deer feces collected in winter and spring than in feces collected in summer and autumn. Gastropods, collected June - October 1995 and June - August 1996, were most abundant in lowland areas (predominantly mixed conifer - deciduous habitat). Canonical correspondence analysis showed that % canopy cover, soil type, and soil depth best explained the distribution of snails among 35 collection sites. Eight of 23 species of gastropods collected were infected with *P. tenuis* larvae; 2 members of the genus *Discus* spp. were considered to be the most important intermediate hosts. Deer concentrated in areas called 'yards' in winter. One such type of yard where deer were fed artificially tended to have more infected gastropods than other areas, but their role in transmission of *P. tenuis* to moose is probably limited for several reasons including that these sites were spatially separated from primary moose range. Another type of yard that involves logging activity poses some threat to moose because numbers of gastropods in it are relatively high and, unlike artificial feeding sites, it is more accessible to moose because of seasonal decreases in human activity.

ALCES VOL. 36: 163-181 (2000)

Key words: *Alces*, deeryards, ecology, gastropods, meningeal worm, moose, *Odocoileus, Parelaphostrongylus tenuis*, transmission, white-tailed deer

Meningeal worm, *Parelaphostrongylus tenuis*, is a parasitic nematode that inhabits the central nervous system of wild ungulates in North America. Infection in white-tailed deer (*Odocoileus virginianus*) (WTD), the main definitive host, is usually benign, whereas infection in other hosts such as moose (*Alces alces*) can be fatal (Anderson and Prestwood 1981, Lankester and Samuel 1998). Meningeal worm is transmitted between ungulate definitive hosts and a variety of terrestrial snails and slugs that serve as intermediate hosts. Gastropods become infected with

[4]Present address: HC-03, Box 347, L'Anse, MI 49946, USA

first-stage larvae deposited into the environment on the fecal pellets of WTD. Ungulates acquire the infection by eating infected gastropods, apparently while foraging.

Fifty-nine moose were translocated from Algonquin Provincial Park, Ontario, Canada, to Marquette County in the western part of Michigan's Upper Peninsula by the Michigan Department of Natural Resources (MDNR) in the mid-1980's. About the same time, numbers of WTD in the region began to increase significantly (Hill 1994, R. W. Aho, Mich. Dep. Nat. Resour., *pers. obs.*). Since then 17 of 53 diagnosed deaths (32%) in moose have been attributed to *P. tenuis*-caused neurological disease (MDNR 1997a). Although the role of *P. tenuis* in limiting population growth of moose in Michigan is not well understood, numbers of moose in the mid-1990's were much lower than predicted despite apparently stable reproductive rates of radio-collared females (Aho 1995, MDNR 1996).

The objectives of the present study were to determine the current status of *P. tenuis* within the WTD population of the Upper Peninsula, the abundance, distribution, and population size of *P. tenuis* in terrestrial gastropods of Baraga County, western Upper Peninsula, and to determine whether or not areas where WTD congregate in winter might serve as foci for infection of WTD and moose.

STUDY AREA

Baraga County (46°80'N, 88°40'W × 46°10'N, 88°00'W) was selected as the main study area because: (1) it encompassed a large portion of the primary range of translocated moose; (2) had a large sympatric population of WTD with associated yarding areas; and (3) had accessible public lands. It is 2,333 km^2 and borders 105 km of Lake Superior shoreline. Dominant forest types are northern hardwoods with scattered communities of spruce-fir (*Picea glauca*, *P. mariana*, *Abies balsamea*), poorly drained lowland hardwoods, and conifer swamp. Baraga County has a cool climate with mean daily temperatures of 15-20°C in July and -10 to -15°C in January. Average annual precipitation between April and September is 54 cm, and average seasonal snowfall is approximately 360 cm, with greater amounts at higher elevations.

Historically, Michigan's Upper Peninsula had few deer because there was little suitable habitat (Bartlett 1938), but numbers exploded to as many as 630,000 in 1949 (MDNR 1996) primarily in response to logging and agricultural practices. Habitat declined and by the mid-1970's, deer densities were as low as 1.2 deer/km^2 (Blouch 1984). Deer numbers began to increase in the 1980's and by autumn 1993, numbers reached an all time high of 740,000 or 17.4 deer/km^2 (Hill 1994). The severe winters of 1995-1996 (~8.8m snow) and 1996-1997 (~8.9m) reduced deer numbers dramatically (PJN, *pers. obs.*). Spring estimates for 1997 were ~370,000 (MDNR 1997b).

Moose, though native to the Upper Peninsula, were few in number when 59 were translocated from Ontario in 1985 and 1987. In 1989, 1991, and 1997, numbers in the western Upper Peninsula were estimated at 124 (Aho and Hendrickson 1989), 210 (Aho 1995), and ~ 100-120 (MDNR 1997c and R. W. Aho, Mich. Dep. Nat. Resour., *pers. comm.*), respectively.

METHODS

The Parasite in White-tailed Deer

In cooperation with MDNR, 158 deer heads were collected from 9 counties in the western Upper Peninsula, from deer killed on roads (Jul - Dec 1995) and deer killed by hunters (Nov - Dec 1995). Heads of deer killed by hunters were collected at meat processing plants or deer check stations and were stored frozen 3 - 5 months until

necropsy at Michigan Technological University, Ford Forestry Center, L'Anse, Michigan. They were cut sagitally using a band saw, then thawed ~ 12 hrs at ~ 20°C. Brain hemispheres were removed and the cavernous, intercavernous, transverse, and sagittal blood sinuses, along with the inner surface of the dura, were examined for adult worms (Prestwood and Smith 1969). Cranial cavities were rinsed and re-examined; water rinsings were examined for adult worms. Worms were carefully collected using small forceps and stored in glycerin (10%) in 70% alcohol (90%).

Deer were aged according to tooth eruption and relative tooth wear as described by Severinghaus (1949) and placed in 3 general categories: fawns (< 1 year old), yearlings (1 - 2 years old), and adults (≥ 2.5 years old). Age and sex of WTD, county of collection, if known, and number of worms were recorded for each deer. Number of worms was determined; when tangled clumps of worms were encountered, counts were based on number of worm tail ends observed using a dissecting microscope (50X).

Prevalence and intensity were compared by age class using G-tests and by collection area (county) using Kruskal-Wallis 1-way analysis of variance (Zar 1984). Statistics were calculated using the Statistical Package for the Social Sciences (Version 7.51, SPSS Inc., Chicago, IL). Results were considered significant at $P \leq 0.05$.

Fecal pellet groups ($n = 218$) from WTD were collected opportunistically from the ground between 21 June 1995 and 30 May 1996. Pellet groups were collected fresh, when either defecation was witnessed or pellets were still moist, or frozen in winter. All groups were stored separately and examined within 5 months of collection. Numbers of samples ranged from 3 to 18 per month. Approximately 20 g feces (range 13.6 - 25.7) per pellet group were examined for dorsal-spined larvae using a modified Baermann technique (Samuel and Gray 1982). Pellets were weighed, wrapped in double-layered cheesecloth, and allowed to stand 24 h in 650 ml water in clean, plastic funnels (20 cm top diam.). Dorsal-spined larvae, both live and dead, were observed using a dissecting microscope at 25X and counted at least twice or until 2 consecutive totals differed < 10%. Counts were averaged for the total number of larvae. Numbers of larvae were reported as larvae per gram (lpg) of fecal pellets.

To avoid contamination between pellet groups, funnels were cleaned with soap and hot water while being scrubbed with a bottlebrush, rinsed with 95% ethanol, and rinsed again with hot tap water. Plastic petri dishes were cleaned in the same manner. The bottlebrush was washed similarly and allowed to soak in a 15% bleach solution at least 24 h between trials. Funnels were tested for contamination, at random, by setting up Baermann funnels containing plain water, processing them the same as fecal pellet solutions, and examining for larvae. No larvae were recovered from cleaned Baermann apparatus ($n = 25$).

Numbers of lpg were compared between seasons using Kruskal-Wallis 1-way ANOVA. Dunn's post-hoc test was used to determine during which seasons lpg differed from each other (Zar 1984).

Not all dorsal-spined larvae in feces of WTD are *P. tenuis*. To attempt to determine whether or not other nematode species occurred in WTD from the Upper Peninsula, 5 entire backstraps (*longissimus dorsi* muscles) and 1 hindquarter from 5 deer (either hit by vehicles or that died in winter) were examined for adult muscleworm, *Parelaphostrongylus andersoni*, using methods described by Prestwood (1972) and Pybus and Samuel (1984). Three of these deer were examined

for adult *P. tenuis* and feces of all 5 were examined for dorsal-spined larvae.

The Parasite in Terrestrial Gastropods

Gastropods were collected in Baraga County at 22 and 13 sites in 1995 and 1996, respectively. Sites in 1995 were selected according to 4 broad types of habitat; mixed conifer/deciduous (n = 7), predominately conifer (n = 4), predominately deciduous (n = 8), and grass (n = 3). Classification was based on the number and ratio of trees (conifer-to-deciduous) along 100 m transects where gastropods were collected. Sites were also selected according to 'definitive host-use categories,' which were; areas where deer concentrated during winter 1994 - 1995 (i.e., deer yards - see below) and summer 1995 (i.e., along roadsides) (n = 8), areas where moose were known to inhabit, but with very little sign of deer activity during spring/summer (i.e., transmission period of *P. tenuis*) (n = 4), and areas with few deer and no signs of moose, hereafter termed 'miscellaneous' (n = 10). Areas where deer concentrated had signs of deer such as deer trails, fecal pellets, or visible concentrations of deer. Areas where moose were known to inhabit were located according to geographical bearings acquired by MDNR from radio telemetry and confirmed by presence of tracks and/or signs of browsing. Miscellaneous sites were originally selected by habitat type and had no large concentrations of WTD and no signs of moose.

Sites in 1996 were: 5 areas called "yards" where deer concentrated during winter, 1995 - 1996, 4 areas where moose had been located the previous summer and/or current spring, and 4 repeat sites from 1995, which included 1 deer yard. Results for the 4 repeat sites were compared to 1995 results for the same time period in 1996 to see if gastropod composition had changed following the harsh winter of 1995 - 1996 (see above, PJN, *pers. obs.*). Sites in 1996 were selected primarily according to use by deer or moose, therefore vegetative descriptions were completed secondarily. Nonetheless, as in 1995, broad categories of habitat were mixed conifer-deciduous sites (n = 4), predominantly conifer sites (n = 4), predominantly deciduous sites (n = 3), and grass (n = 2).

Habitat surveys of sites were completed 10 - 21 August 1995 and 1996. Data were gathered at 20 m intervals (i.e., where gastropods were collected; see below) along 100 m transects. Data recorded at each location were number and identification of trees in a 4 m circle including diameter at breast height (dbh) for trees >2 cm dbh, number and identification of plant species on the ground in a 1 m^2 area, depth (cm) of soil (AH layer) and averaged for the site, and percent canopy cover averaged for the site and rounded to the nearest 10%. Plant species were identified using various field guides (Voss 1972, 1985; Newcomb 1977; Barnes and Wagner 1981). Vegetation surveys were limited to immediate areas where gastropods were collected. Additional soil characteristics such as soil type, permeability, and approximate depth of the water table were obtained from soil surveys for Baraga County conducted by the Soil Conservation Service of the United States Department of Agriculture (Berndt 1988).

Gastropods were collected at 20 m intervals along 100 m permanent plot transects, with 1 transect per site. To attract gastropods, corrugated cardboard (1 m^2) was placed at each interval (Boag 1982, 1990). In 1995, collections were done weekly from 05 June to 30 August and biweekly from 1 September to 11 October. In 1996, collections were done weekly 10 June to 12 August. Cardboards were moistened on the evening prior to collection to attract gastropods and covered with plastic sheeting to slow evaporation. They were examined

between 0600 and 1100 h, or between 0800 and 1300 h during periods of rainfall, when they were still moist. Gastropods were removed from both sides and the inner layer of the cardboard, and from both sides of the plastic sheets. Cardboards were replaced when they became too ragged to manipulate or if destroyed by animals. Replacement cardboards were placed on the same spot or directly adjacent if a large amount of mold was present. Cardboards placed in repeat collection sites for 1996 were staggered, approximately 10 m, between previous cardboard placements of 1995.

Snails and slugs were placed in plastic boxes with small compartments, lined on the inside cover with moist cheese-cloth to avoid desiccation, and stored on ice in a plastic cooler for transport. Gastropods were stored separately by collection area 24 - 48 h at approximately 9°C and sorted by species prior to the digestion process. Gastropods were identified using keys in Burch (1962), Burch and Jung (1988), and Burch and Pierce (1990). Dr. John Burch, The University of Michigan, Ann Arbor, verified identifications of gastropods.

Once identified, gastropods were placed in small 5-ml test tubes, 1 - 4 per tube of the same species and collection area. Slugs and larger species of snails were minced with a scalpel or fine scissors before placing them in 50-ml tubes. Three to 4.5 ml of artificial digesting solution (0.7 ml concentrated HCl and 0.6 gm pepsin powder per 100 ml distilled water, Samuel *et al.* 1985) were added to each 5 ml test tube, while 6 - 8 ml were added to the 50 ml tubes. Gastropods were crushed with wooden sticks and the solutions stirred vigorously. During preliminary trials, different sizes of gastropods were incubated for varying periods of time at 38 - 40°C. Eight hr was the optimal incubation time for all gastropods except the large snail, *Triodopsis albolabris*, which incubated 16 hr. All tubes were agitated at least once during incubation to assist breakdown of the tissue. Following incubation each tube of solution was examined individually, rinsing the liquid into small 6-cm plastic petri dishes and viewed at 25X using a dissecting microscope. Dishes remained untouched approximately 3 min, which allowed larvae to settle to the bottom of the dish.

Large numbers of gastropods were collected, which occasionally required pooling of individuals prior to digestion. Previous studies have handled the problem of multiple larvae from pooled gastropods by assuming that all larvae came from 1 snail (Whitlaw *et al.* 1996). Although this is a reasonable assumption in cases of low overall prevalence, it is not a certainty. Therefore, in the end, we excluded data from test tubes with multiple gastropods and multiple larvae for all calculations. The result was a slightly lower prevalence in 1995 and 1996 (0.5% and 1.1%) than had we followed Whitlaw *et al.* (1996) (0.6% and 1.6%, respectively). The trade-off was more accurate data for intensity of infection per gastropod, because we do not believe one can assume that all larvae come from 1 snail unless very few larvae are found.

Two species of slugs, *Arion fasciatus* and *A. subfuscus*, were collected (511 total) during June 1995. Slugs of this genus have a thick coating of slime and exceptionally firm tissue of the foot so they are probably poor intermediate hosts of *P. tenuis*. Despite the fact that these introduced slugs are fairly common throughout northeastern North America (Getz and Chichester 1971), only 1 individual of the species *Arion circumscriptus* has been found infected with *P. tenuis* (Lankester and Anderson 1968). In addition to their low potential for infection, it took many hours to digest these slugs artificially. None of the 511 *A. fasciatus* and *A. subfuscus* collected in June 1995 and examined for *P.*

tenuis was infected. For these reasons the genus *Arion* was not collected after June 1995 and data for it are not included in any analyses or results.

Two species of snails, *Discus cronkhitei* and *D. catskillensis*, look nearly identical except for subtle differences in the shape of the shell (Burch 1962). Both species were abundant and found together often. It took much time to separate these species, so they were recorded as *Discus* spp. collectively.

Larvae were collected, a majority alive and moving, using a 1 cc syringe and large gauge needle with the beveled tip removed. They were placed in 4-ml vials with approximately 3 ml of 10% glycerin-alcohol that was heated to near boiling in a microwave oven immediately prior to addition of larvae. Using a microwave to heat the glycerin-alcohol caused problems wherein some larvae coiled tightly and esophagi buckled. It is possible to kill and properly preserve larvae simultaneously (Platt 1978, Samuel *et al.* 1985), but using a microwave oven to heat the alcohol solution was ineffective. Potential *P. tenuis* larvae were excluded because of difficulty identifying crucial characteristics, therefore numbers of larvae in gastropods are conservative estimates.

Normally, third-stage larvae of *P. tenuis* are large (minimum about 900 mm), relatively translucent and die in a characteristic "c" shape (Anderson 1963). Large larvae that fit the classic description (Anderson 1963) were assumed to be those of *P. tenuis*. However, some larvae were smaller and granular in appearance because they were killed in alcohol heated by microwave. Therefore, drawings were made from a random subsample of larvae (n = 97) with the aid of a compound microscope, in direct light and/or phase contrast settings, with a camera lucida attachment. Measurements of total length and distinguishing characteristics were taken from the drawings using a Summa Sketch Plus digitizing tablet (Summagraphics Corp., Fairfield, CT). For smaller distorted larvae (700 - 799 μm), locations of the various body parts were measured as percent of the total body length. Larvae were considered *P. tenuis* if they fit the classic descriptions or had at least 4 of the 5 following characteristics: (1) shape of the buccal capsule; (2) correct location of the nerve ring; (3) correct location of the excretory pore; (4) correct location of the terminal end of the esophagus; and (5) presence of a small constriction at the tip of the tail. Larvae that were ≤ 699 μm or too tightly coiled to see defining characteristics were excluded from the data set.

Measurements from the subset of larvae were confirmed by comparing them to measurements of *P. tenuis* made by Anderson (1963) and Ballantyne and Samuel (1984). In addition, all specimens were compared to known third-stage larvae of *P. tenuis* that were reared in laboratory-raised (*Triodopsis* spp.) snails at the University of Alberta and more from Lakehead University. Laboratory-raised snails and larvae were processed using the same techniques for specimens collected from the field sites.

Analyses of gastropod data by years were conducted separately because criteria for site selection differed between 1995 and 1996, and the collection season for 1995 was 6 weeks longer than for 1996. One-way ANOVA or t-tests were calculated when data expressed constant variance, normal distribution, and if power of the analyses were at least 0.80 at P = 0.05. Differences between multiple categories were determined using Tukey's Honestly-Significant-Difference multiple comparison test (Zar 1984). If data did not pass normality or variance tests, Kruskal-Wallis 1-way ANOVA or Mann-Whitney-U statistics were then used and differences were determined using Dunn's multiple comparison

test (Zar 1984).

To see what components of habitat best explained the distribution of gastropods between collection sites, canonical correspondence analysis (CCA) was done using Canonical Community Ordination (CANOCO) computer software (ter Braak 1987a) for both 1995 and 1996. CCA is useful because it offers visual ordination diagrams that express spatial patterns of floristic, and in this case, gastropod composition. Ordination determines the order of variance in abundance of species data explained by linear combinations of environmental variables (ter Braak 1987b). Abundance of species data were modified by natural log transformation to correct for large numbers of zeroes in the data set (ter Braak 1987a) and rare species were down-weighted for more accurate correlation. Percent canopy cover (CC), depth of topsoil (SD), soil type (ST), permeability of soil (PM), and depth of water table (WT) were 5 environmental variables used in the analyses.

RESULTS

The Parasite in White-tailed Deer

Sixty-nine of 158 (44%) deer examined had adult *P. tenuis*. Prevalence by county ranged from 29 % to 65 %. There was no difference in prevalence for the 3 counties, Baraga, Iron, and Marquette, that encompassed the primary range of translocated moose and offspring (23 of 59, 39%), and that for counties nearby (46 of 99, 46%) (G = 13.4, 9 df, $P > 0.10$). Prevalence was significantly lower in fawns (28% of 51; G = 8.3, 2 df, $P < 0.025$) than in yearlings (52% of 42) or adults (51% of 65). Fawns had significantly fewer worms (all with 1 worm, H = 12.6, 2 df, P = 0.002) than did yearlings ($\bar{x}$ = 2.0, SD = 1.4, n = 42) or adult deer ($\bar{x}$ = 1.9, SD = 0.9, n = 65). Intensity of infection did not differ between counties (H = 16.7, 9 df, P = 0.06). The overall mean intensity was 1.7 (SD = 1.1) worms (range 1 - 5). Forty of the 69 infected deer had 1 worm.

There was no significant difference in prevalence of adult worms between deer genders (43% of 124 females, 47% of 34 males, G = 0.20, 1 df, $P > 0.50$). Intensity was also similar between females ($\bar{x}$ = 1.77, SD = 1.05) and males ($\bar{x}$ = 1.63, SD = 1.15).

Sixty-three percent (137/218) of deer pellet groups had dorsal-spined larvae. Mean numbers of larvae per g feces (± SD) during summer, autumn, winter 1995, and spring 1996 were 16.4 (± 29.7), 22.1 (± 41.3), 66.1 (± 95.9), and 114.4 (± 189.9), respectively. Larvae per g of feces differed significantly by season with highest mean numbers in winter and spring (H = 29.5, 3 df, $P < 0.001$).

No *P. andersoni* were found in the musculature of 5 WTD. One of the 5, an adult female killed on a road and collected February 1997, had dorsal-spined larvae in the feces. The head was heavily damaged and not examined for *P. tenuis*. No *P. tenuis* were found in 3 heads of the 5 WTD examined.

The Terrestrial Gastropods

A total of 9,477 gastropods representing 12 families, 19 genera, and 23 species, were collected in 1995 and 1996 (Table 1). *Zonitoides arboreus* was the most common species, accounting for 36% of the gastropods collected. In 1995, but not 1996, mean numbers of gastropods per site (± SD) were significantly higher in mixed conifer-deciduous habitat (1995, 477 ± 236; 1996, 366 ± 225) than in predominantly conifer (1995, 179 ± 144; 1996, 219 ± 183), predominantly deciduous (1995, 175 ± 96; 1996, 311 ± 103), or grass habitats (1995, 150 ± 6; 1996, 191 ± 62)(1995, H = 10.1, 3 df, P = 0.02; 1996, H = 2.5, 3 df, P = 0.47). Abundance of gastropods did not differ between areas with concentrations of deer (350 ± 306), areas inhabited by moose (215 ± 121), or miscellaneous sites (237 ± 118) in 1995 (H = 0.3, 2 df, P = 0.86), but in 1996

Table 1. Numbers of gastropods collected and infected with *Parelaphostrongylus tenuis* by species, 1995 and 1996. Underlined letters in species names represent abbreviations used in Figure 2.

Species	Prevalence[1] 1995	1996	Total	Intensity (mean) 1995	1996	Total
Order Geophila						
Suborder Sigmaurethra						
Family Discidae						
Discus spp.[2]	11/854(1.3)	15/704(2.1)	26/1558(1.7)	1.2	1.7	1.5
Anguispira alternata	1/225(0.4)	3/161(1.9)	4/386(1.0)	1.0	4.3	1.5
Family Helicodiscidae						
Helicodiscus parallelus	0/66	0/44	0/110	0	0	0
Family Vitrinidae						
Zonitoides arboreus	5/2102(0.2)	8/1317(0.6)	13/3419(0.4)	1.0	1.0	1.0
Zonitoides nitidus	3/149(2.0)	1/91(1.1)	4/240(1.7)	3.3	8.0	4.5
Nesovitrea electrina	0/12	0/42	0/54	0	0	0
Striatura exigua	0/408	0/71	0/479	0	0	0
Striatura ferrea	0/53	0/7	0/60	0	0	0
Vitrina *limpida*	0/1	0/19	0/20	0	0	0
Family Limacidae						
Deroceras laeve	4/424(0.9)	5/236(2.1)	9/660(1.4)	1.0	4.0	2.7
Deroceras reticulatum	0/120	0/103	0/223	0	0	0
Family Punctidae						
Punctum minitusum	0/91	0/8	0/99	0	0	0
Family Phylomycidae						
Pallifera dorsalis	3/232(1.3)	2/131(1.5)	5/363(1.4)	1.7	2.0	1.8
Family Mesodontidae						
Immature Mesodontidae	0/15	0/35	0/50	0	0	0
Triodopsis albolabris	2/7(29)	4/6(67)	6/13(46)	1.0	7.5	5.3
Strenotrema fraternum	0/10	0/10	0/20	0	0	0
Family Euconulidae						
Euconulus fulvus	0/96	0/14	0/110	0	0	0
Suborder Orthurethra						
Family Cionellidae						
Cionella lubrica	1/808(0.1)	0/476	1/1284(0.1)	1.0	0	1.0
Family Vallonidae						
Vallonia excentrica	0	0/7	0/7	0	0	0
Zoogenetes harpa	0/36	0/3	0/39	0	0	0
Family Pupillidae						
Columella edentula	0/5	0	0/5	0	0	0
Vertigo tridentata	0/41	0/1	0/42	0	0	0
Family Strobilopsidae						
Strobilops labrynthica	0/125	0/111	0/236	0	0	0
Total	30/5880(0.5)	38/3597(1.1)	68/9477(0.7)	1.4	2.9	2.2

[1]Number examined/number infected (% infected)
[2]*Discus* spp. = *D. cronkhitei* and *D. catskillensis*

there were more gastropods in deer yards (415 ± 154) than in areas inhabited by moose (149 ± 69) (t = 3.1, 8 df, P = 0.01). Repeat collection sites had similar mean numbers of gastropods both years (1995, 198 ± 99; 1996, 175 ± 46). Only 3 of 2,046 gastropods from 4 sites sampled in both years were infected.

Variation in abundance of particular species of gastropods between different habitat types was best explained in 1995 by canopy cover, soil type, and permeability of the soil; in 1996 by canopy cover and soil depth (Table 2). The first two axes of the ordinations explained 61% of the variation in the species-environment relationship in 1995 and 65% for 1996. Axes 3 and 4 explained little additional variance and were not included in the ordination diagrams for either 1995 or 1996. Axis 1 correlated with % canopy cover (1995, t = 8.40, df = 16, P < 0.001; 1996, t = 8.80, df = 7, P < 0.001) so the left side of the ordinations represented shaded conditions and the right side represented more open conditions (Fig. 1). For 1995, Axis 2 correlated with soil type (t = 2.17, df = 16, P < 0.02) and permeability (t = 2.35, df = 16, P < 0.05), which defined a moisture gradient. Therefore, the top half of Axis 2 represented soils of loam or muck and lower permeability versus the negative side of Axis 2, which represented sandier soil types and higher permeability (Fig. 1). All sites in 1996 were relatively moist, so soil depth correlated with axis 2 as the defining characteristic (t = 5.13, df = 7, P < 0.002). Deeper soils were represented on the negative side of axis 2 (Fig. 1).

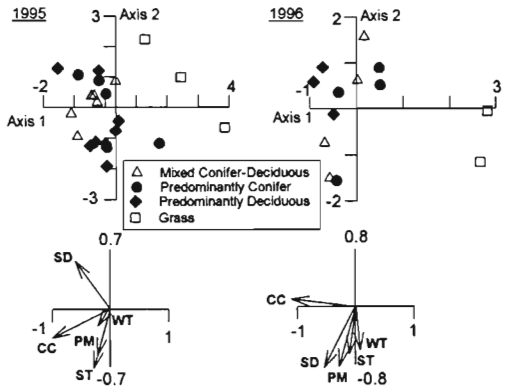

Fig. 1. Site distributions that include habitat types from canonical correspondence analyses, 1995 and 1996. Corresponding environmental variables used in the analyses are shown on lower graphs. CC = canopy cover, PM = permeability, SD = soil depth, ST = soil type, WT = depth of water table.

In 1995, 3 of the 4 broad habitat types showed as relatively distinct groups in the ordination and followed a moisture gradient (Fig. 1). Most mixed sites were generally lowland areas with deep topsoil of loam and moderate permeability. This moisture gradient was not well defined in 1996 because all sites were in moist areas. However, some mixed sites and conifer sites had deeper topsoil.

Most importantly in both 1995 and 1996, gastropod distribution showed similar asso-

Table 2. Summary of canonical correspondence analysis involving 5 environmental variables for 35 sites where data on gastropods and species of vegetation were collected

	1995		1996	
Axis	1	2	1	2
Eigenvalue	0.30	0.17	0.45	0.24
Species/Environment Correlation	0.93	0.92	0.97	0.97
Cumulative % Variance				
of Species Data Explained	12.6	19.4	22.6	34.6
of Species-Environment Relation	39.7	61.4	42.5	64.8

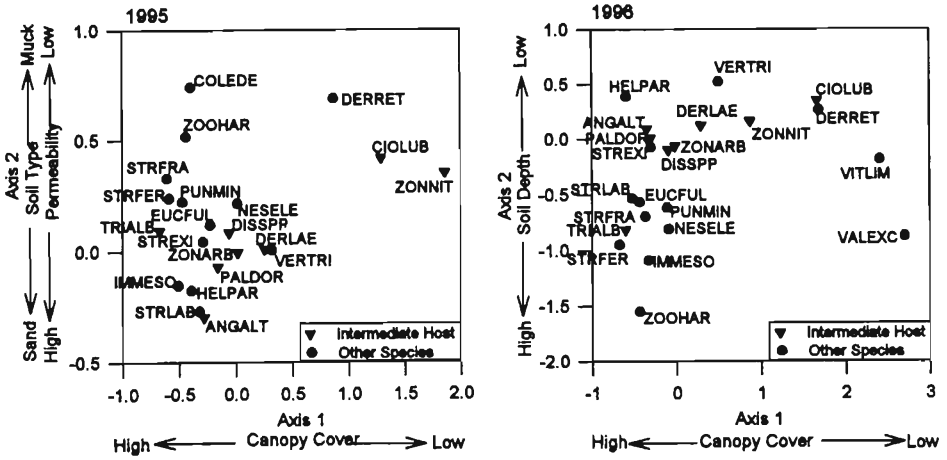

Fig. 2. Spatial distribution of gastropod species in relation to environmental variables, 1995 and 1996. Abbreviations of species names are underlined in Table 1.

ciations with particular habitat types and environmental variables (Fig. 2). The most widely distributed species of gastropods in both years were *Zonitoides arboreus* (found at all 35 collection sites), *Discus* spp. (34 sites), *Deroceras laeve* (34 sites), and *Pallifera dorsalis* (30 sites). These species clustered near zero in the ordinations, which represent their common occurrence in most sites, therefore we could not determine distinct habitat factors that affected their distribution. However, *Cionella lubrica*, *Zonitoides nitidus*, and *Deroceras reticulatum* were closely associated with wet habitats lacking canopy cover and *Anguispira alternata* and *Helicodiscus parallelus* were associated with relatively drier deciduous sites and more canopy cover in both years (Fig. 2).

In 1995 and 1996, *Striatura exigua*, *Euconulus fulvus*, *Striatura ferrea*, *Strenotrema fraternum*, *Zoogenetes harpa*, and *Punctum minitusum* comprised a group that were often found together and associated with predominantly conifer and mixed composition habitats with deep topsoils. Strong associations between particular species of vegetation and gastropods were not clearly identified except for the potential affinity of these conifer-related species to areas with eastern hemlock and northern white cedar. *Triodopsis albolabris* was found only in mixed forest stands.

The Parasite in Terrestrial Gastropods

Larvae of *P. tenuis* were found in 68 of 9,477 (0.7%) gastropods in 1995 - 1996 (Table 1) representing 8 species of gastropods, *Triodopsis albolabris*, *Discus* spp., *Zonitoides nitidus*, *Deroceras laeve*, *Pallifera dorsalis*, *Anguispira alternata*, *Zonitoides arboreus,* and *Cionella lubrica.* Mean intensity was 2.2 (SD = 2.9, range = 1 - 19) with highest intensity occurring in *T. albolabris* and *Z. nitidus.*

Numbers of infected gastropods did not differ among habitat types in 1995 (H = 3.03, 3 df, P = 0.39) or 1996 (H = 4.3, 3 df, P = 0.23). In 1995 there were more infected gastropods in areas where deer concentrated (2.4 ± 1.8 SD) than in areas that were inhabited by moose (0.7 ± 0.9 SD), or in miscellaneous sites (1.0 ± 1.4 SD) (H = 5.42, 2 df, P = 0.06). In 1996 there were more infected gastropods in deeryard areas (5.3 ± 6.3 SD) than in areas inhabited by moose (1.3 ± 1.0 SD) (U = 13.5, n_1 = 4, n_2 = 6, P = 0.07).

A total of 248 larvae from gastropods,

55 in 1995 and 193 in 1996, were identified as *P. tenuis*. A majority of the larvae were collected alive and their movement and general appearance were similar to 'known' *P. tenuis* larvae from laboratory-raised snails. Measurements from 97 of these preserved larvae were compared to larvae from laboratory-raised snails and results were similar. Also, many direct measurements fit within ranges from previous studies (Anderson 1963, Ballantyne and Samuel 1984), but specimens that distorted following preservation were identified by defined characteristics measured as percent of total length (Anderson 1963). Second-stage larvae were differentiated from third-stage larvae by the presence of a double cuticle with the dorsal spine still visible. Seventy-eight of 248 larvae (31%) were identified as second-stage larvae.

In 1995 and 1996, total numbers of larvae (second and third stage) were similar among the 4 broad habitat types (1995, H = 2.36, 3 df, P = 0.50; 1996, H= 4.09, 3 df, P = 0.25). In 1995 and 1996, mean numbers of larvae were slightly, but not significantly, higher in gastropods collected in areas frequented by deer in 1995 (4.7 ± 4.9) or deer yards in 1996 (25.8 ± 25.3) than from areas inhabited by moose (1995, 1.3 ± 1.6; 1996, 6.0 ± 6.5) (1995, H = 5.23, 2 df, P = 0.07; 1996, t = 1.95, 8 df, P = 0.08).

DISCUSSION

Overall prevalence of adult *P. tenuis* in WTD in this study (44%) is similar to that for most other studies in the Great Lakes region: Michigan (46 and 57%, DeGiusti 1955, 1963, respectively), Ontario (33 and 41%, Anderson 1956, 1963), Minnesota (33, 49, and 82%, Loken *et al.* 1965, Karns 1967, Slomke *et al.*. 1995, respectively), Wisconsin (38, 58, and 38%, Samuel and Trainer 1969, Dew 1988, Boppel 1994, respectively), and southeastern Manitoba (54%, Wasel 1995). Our finding of 63% prevalence of dorsal-spined larvae in feces of WTD is also similar to that for studies done previously in the Upper Peninsula. Schmitt *et al.* (1983, 1987, 1988, 1989) reported the annual % prevalence of dorsal-spined larvae (assumed to be *P. tenuis*) in feces of WTD from the Upper Peninsula as 76, 65, 65, and 59, respectively. These prevalences are all higher than the prevalence of adult worms in WTD crania, suggesting that we either overlooked some worms during necropsy or that other nematodes closely related to *P. tenuis* (e.g., *Parelaphostrongylus andersoni* or *Varestrongylus alpenae*) are present. We did not find *P. andersoni* during examination of several WTD, but its presence in WTD of the Upper Peninsula was implied by Pybus *et al.* (1990).

Varestrongylus alpenae occurs in lungs of WTD and the larva is similar in appearance to that of *P. tenuis*. Adults are very difficult to detect because of their small size, cryptic location and lack of lesions in lung tissue (Gray *et al.* 1985). We did not look for *V. alpenae* but Dikmans' original description of it (1935) is based on specimens collected from WTD in Michigan's Upper Peninsula.

Implications for Gastropods in Transmission of *P. tenuis*

Although few species of gastropods in the Upper Peninsula were infected with *P. tenuis* larvae, those most widely distributed in the study area were important intermediate hosts for *P. tenuis*. This is consistent with results from studies elsewhere (Lankester and Anderson 1968, Maze and Johnstone 1986, Upshall *et al.* 1986, Rowley *et al.* 1987, Platt 1989). Based on an importance value calculated for each infected species (mean intensity of infection × prevalence of infection × proportion of total gastropods × 100) (Leong and Holmes 1981, Margolis *et al.* 1982), we determined

that the most important hosts for *P. tenuis* in Michigan's Upper Peninsula were *Discus* spp., found at 34 of 35 collection sites and in all habitat types, *Triodopsis albolabris*, *Deroceras laeve*, and *Zonitoides nitidus*. *Deroceras laeve* was widespread (34 sites representing all habitats), but *Z. nitidus* and *T. albolabris* were neither numerous nor widespread (240 and 13 individuals collected at 6 and 7 sites, respectively). Importance values of *Z. nitidus* and *T. albolabris* were relatively high because of high intensity (*Z. nitidus*) or prevalence and intensity (*T. albolabris*). *Deroceras laeve* and *Z. nitidus* are known important hosts of *P. tenuis* in Ontario (Lankester and Anderson 1968). Members of the genus *Triodopsis* have been found in low numbers, but with high prevalence and/or intensities of infection, in previous studies (Maze and Johnstone 1986, Rowley *et al.* 1987, Raskevitz *et al.* 1991).

Results from this and other studies indicate that lowland areas, which tend to be in mixed conifer-deciduous habitat, have more gastropods than other areas (Clarke *et al.* 1968, Getz 1974, Gleich and Gilbert 1976, Kearney and Gilbert 1978). This supports the idea that moisture is an important requirement for gastropod communities (Walton 1963, Boag 1985, Prior 1985). It also explains why abundance of gastropods was greater in mixed sites in 1995 but similar between habitat types in 1996, when all collection sites were in moist lowlands. *Cionella lubrica*, *Z. nitidus*, and *Deroceras reticulatum* were found often near standing water (this study, Lee 1952, Clarke *et al.* 1968, Andersen and Halvorsen 1984). These known intermediate hosts of *P. tenuis* could have serious implications for transmission to moose if they are found along edges of wetland areas that moose frequent in summer.

Although moisture probably affects the distribution of many gastropod species, one intermediate host, *Anguispira alternata*, was found in drier upland stands of predominantly deciduous or mixed composition and "'...seems capable of enduring the driest situations"' (Latchford 1885 as cited by Clarke *et al.* 1968). *Zonitoides arboreus* was also present in high numbers at these sites, suggesting that some intermediate host species do not require high moisture regimes.

Overall, intermediate hosts of *P. tenuis* were found in all habitat types. Although moisture was a requirement for most gastropods, 2 intermediate hosts were found in dry upland areas as well. Many of the most wide-ranging species serve as intermediate hosts but those associated with wet open habitat may pose a serious risk to moose feeding in wetland areas during summer because of the snails' affinity to mud and water.

Implications for Moose

With nearly half the WTD in the study area infected with *P. tenuis* and important intermediate hosts found in all types of habitat, the potential for moose to become infected with meningeal worm seems high. This is particularly true for young moose that might disperse from the relative safety of higher elevations to the surrounding lower elevations with high deer densities and more areas where deer congregate in winter (i.e., deer yards).

A main goal of the present study was to examine the idea that deeryards might serve as foci for transmission of *P. tenuis* to WTD and moose. The idea is not new (Lankester and Peterson 1996, Whitlaw *et al.* 1996), but it is fascinating for many reasons including: yarding behavior is common for WTD populations in the Great Lakes region; meningeal worm is likely present in WTD in all deer yards; some yards occur within moose range; deer often remain in yards when numbers of worm

larvae shed in deer feces are at their annual high between February and May (Peterson *et al.* 1996, this study); though many larvae shed in WTD feces in winter, die (Forrester and Lankester 1998), some survive freezing (Lankester and Anderson 1968, Shostak and Samuel 1984); and gastropods that serve as intermediate hosts are likely present in most deer yards (this study, Lankester and Peterson 1996).

To illustrate better the potential for deeryards to become focal areas for infection, the following is a presumptive calculation of dorsal-spined larvae potentially deposited in deeryards. Adult, free-ranging, female WTD in northeastern Minnesota defecate an average of 22 times/d, January through April (Rogers 1987). In the present study, the average wet weight of 19 pellet groups (presumably from adult deer) collected between January and April was 62.2 g (SD = 7.7). This extrapolates to ~ 1,370 g feces/d/adult female deer. We found that deer shed an average 65.5 larvae/g feces (Jan - Apr), which means that a WTD could shed as many as ~ 90,000 larvae daily. By extrapolation 1 infected deer in Michigan's Upper Peninsula could shed several million larvae (actually, 10.8 million larvae using the previous estimates) between January and April. Even if ~75% of these larvae die by early spring (Forrester and Lankester 1998), there are several million (2.7 million by extrapolation) larvae per infected adult deer that could survive and possibly infect gastropods.

The ability of a deer yard to act as a focal area of infected gastropods probably depends on many factors including the habitat type and resulting species of gastropods present, density of deer, whether or not the yard is used by deer in winter on an annual basis, variable weather conditions, etc. The potential danger that these yards pose to deer and moose also depends on whether or not yards will be visited during the snow-free part of the year when transmission takes place.

The Upper Peninsula including Baraga County has 3 types of deer-yarding areas: natural, created by logging operations, and those created by artificial feeding of WTD. Within the study area most yards are located at lower elevations near Lake Superior. White-tailed deer live in and around all 3 types of yards throughout the year although many deer disperse to upland sites in the interior of Baraga County in summer. Currently, moose are not abundant in areas of low elevation, but are seen occasionally along Lake Superior during spring and autumn (R. W. Aho and PJN, *pers. obs.*).

Historically, naturally occurring yards were most common. They were and are comprised almost entirely of swamp-conifer tree species such as northern white cedar (*Thuja occidentalis)* and eastern hemlock (*Tsuga canadensis*). WTD tend to feed in nearby upland stands and use conifer-yards primarily for protection from adverse weather (Van Deelen *et al.* 1996). Despite critically low browse availability, deer return to these same conifer stands annually until the stand loses its ability to maintain a stable microclimate (Verme 1965). As determined by ordinations in this study, gastropod intermediate hosts were found in habitat that was predominantly conifer, but the most abundant species in this environment were not known intermediate hosts. Therefore, these naturally occurring deeryards likely present little threat as foci for transmission of meningeal worm to moose because they lack sufficient numbers of intermediate host species.

WTD also congregate during winter in areas where timber is harvested. Such areas are mobile in the sense that deer move when logging operations move. Two of the 31 sites for collection of gastropods were in logged deeryards; they provided 10% of the gastropods collected in this

study and 14% of the infected gastropods. A large proportion of logging in Baraga County occurs in mixed conifer-deciduous stands in winter and is mostly a selective-cutting method rather than clear-cut (PJN, *pers. obs.*). Selective-cutting leaves behind slash material and areas of shade that potentially enhances the habitat for gastropods. In addition to good snail habitat, deeryards that center on logging operations are more accessible to moose because they have little human use much of the year.

A more general concern is that the amount of logging within primary moose range appears to be increasing (PJN, *pers. obs.*), thus attracting and potentially holding WTD through winter and into early spring when greatest numbers of worm larvae are deposited with deer feces. The combination of remote locations and potentially enhanced snail habitat suggests that deer yards centered on logging, particularly within moose range, pose the greatest threat to moose.

A third type of deeryard created by artificial feeding is common in the Upper Peninsula. Most feeding takes place during winter and spring, and deer at such sites become accustomed to people. During our study, feeding sites were usually close to human-populated areas so that people could watch deer feed. Seven of our 31 collection sites for gastropods were associated with areas where deer were fed artificially. In total, 36% of gastropods collected, and 34 of the 68 infected gastropods, were from these artificial feeding sites. One 1996 collection site, with on-site feeding and a logging operation nearby, provided only 347 (3.7%) of the 9,477 gastropods collected during the study, but 18 (26%) of the 68 infected gastropods. Approximately 200 deer were fed in a 3 ha area at this site; the ground was covered with a dense layer of deer fecal pellets. Yards where WTD are fed artificially are likely a focus of transmission of *P. tenuis* to resident WTD, but pose limited threat to moose because few moose frequent such areas, at least currently.

From the perspective of accidental ingestion of infected gastropods during foraging, moose and deer feed differently throughout the year. Diets of WTD mostly consist of succulent ground-level foods from spring to autumn (Skinner and Telfer 1974). These foods include herbs, grass, ferns, fruit and mast, and fungi (Skinner and Telfer 1974, Weckerly and Kennedy 1992). Potentially infected gastropods could be associated with any of these foods. Conversely, moose prefer browse throughout the year (Renecker 1987, Renecker and Schwartz 1998) and we expect that fewer terrestrial gastropods would be associated with browse. However, autumn is when moose consume much ground-level vegetation (Renecker and Schwartz 1998) including relatively large quantities of leaf litter (Renecker and Hudson 1986, Renecker 1987). Thus, autumn is probably when moose are at maximum risk of acquiring meningeal worm infection through accidental ingestion of infected gastropods.

Although data from this study suggest that most transmission to ungulates occurs in late summer and autumn, spring transmission is possible (Lankester and Anderson 1968, Platt 1989). Infective third-stage larvae were found in gastropods collected in June during the current study; these gastropods almost certainly survived the previous winter.

In summary, *P. tenuis* is prevalent in WTD from Baraga County and from counties nearby. Infected gastropods occur throughout the various habitat types in the study area. Deeryards in general probably pose minimal risk for transmission of *P. tenuis* to moose except for those located where logging occurs and within primary moose range. Moose are probably most vulnerable to acquiring *P. tenuis* during

autumn because of changes in diet. Our data suggest that meningeal worm has the potential to limit growth of this translocated population.

ACKNOWLEDGEMENTS

This study was funded by Michigan Department of Natural Resources (MDNR) through Federal Aid in Wildlife Restoration, Michigan Pittman-Robertson Project W-127-R, Natural Sciences and Engineering Research Council of Canada (operating grant to WMS), and the Department of Biological Sciences, University of Alberta (teaching assistantship awarded to PJN). Michigan State University managed MDNR funds and provided use of a truck; Michigan Technological University provided a place to live and laboratory space at the Ford Forestry Center, Alberta, MI; MDNR provided various equipment; and The Snow Drifters Snowmobile Club provided use of a snowmobile. We thank Rob Aho, MDNR biologist from Baraga, for introducing PJN to the area and providing encouragement, kindness, equipment, and valuable information regarding the local moose population; Murray W. Lankester, Lakehead University (Thunder Bay, Ontario), for advice on methods relating to meningeal worm larvae and gastropods; John Burch, University of Michigan (Ann Arbor, MI), for confirmation of gastropod identifications; and Robert Freckman, University of Wisconsin - Stevens Point (Stevens Point, WI), for aid in identifying plants. Special thanks to the following individuals for many services rendered: Coral Johnson (Michigan State University), many MDNR personnel, Jim Dogevito and Dave Stimac (Michigan Technological University), Kurtis Saker (University of Alberta), Clifford Nankervis Jr., and numerous landowners of Baraga County.

REFERENCES

AHO, R. W. 1995. Michigan's translocated moose population: 10 years later. Mich. Dep. Nat. Resour., Wildl. Div., Rep. No. 3245. 18 pp.

_____ and J. HENDRICKSON. 1989. Reproduction and mortality of moose translocated from Ontario to Michigan. Alces 25:75-80.

ANDERSEN, J. and O. HALVORSEN. 1984. Species composition, abundance, habitat requirements and regional distribution of terrestrial gastropods in arctic Norway. Polar Biol. 3:45-53.

ANDERSON, R. C. 1956. *Elaphostrongylus odocoilei* Hobmaier and Hobmaier, 1934 in the cranial case of *Odocoileus virginianus borealis* Miller. Can. J. Zool. 34:167-173.

_____. 1963. The incidence, development, and experimental transmission of *Pneumostrongylus tenuis* Dougherty (Metastrongyloidea: Protostrongylidae) of the meninges of the white-tailed deer (*Odocoileus virginianus borealis*) in Ontario. Can. J. Zool. 41:775-792.

_____ and A. K. PRESTWOOD. 1981. Lungworms. Pages 266-317 *in* W. R. Davidson, F. A. Hayes, V. F. Nettles, and F. E. Kellogg (eds.) Diseases and parasites of white-tailed deer. Tall Timbers Research Station, Misc. Pub. No. 7, Tallahassee, FL. 458 pp.

BALLANTYNE, R. J. and W. M. SAMUEL. 1984. Diagnostic morphology of the third-stage larvae of three species of Parelaphostrongylus (Nematoda, Metastrongyloidea). J. Parasitol. 70:602-604.

BARNES, B. V. and W. H. WAGNER, JR. 1981. Michigan trees: a guide to the trees of Michigan and the Great Lakes Region. Univ. Mich. Press, Ann Arbor, MI. 383 pp.

BARTLETT, I. H. 1938. Michigan's deer problem. Bull. Mich. Dep. Conserv.,

Lansing, MI. 64 pp.

BERNDT, L. W. 1988. Soil survey of Baraga County area, Michigan. U. S. Dep. Agric., Washington, DC. 306 pp.

BLOUCH, R. I. 1984. Northern Great Lakes States and Ontario Forests. Pages 391-410 *in* L. K. Halls (ed.) White-tailed deer ecology and management. Stackpole Books, Harrisburg, PA.

BOAG, D. A. 1982. Overcoming sampling bias in studies of terrestrial gastropods. Can. J. Zool. 60:1289-1292.

_____. 1985. Microdistribution of three genera of small terrestrial snails (Stylommatophora: Pulmonata). Can. J. Zool. 63:1089-1095.

_____. 1990. On the effectiveness of artificial shelters in the study of population attributes of small terrestrial gastropods. Can. J. Zool. 68:254-262.

BOPPEL, P. J. 1994. Meningeal worm in white-tailed deer of Northern Wisconsin with implications for elk. Unpubl. Rep., Univ. Wis. - Stevens Pt., Coll. Nat. Resour., Stevens Pt., WI. 12 pp.

BURCH, J. B. 1962. How to know the eastern land snails. William C. Brown Co. Pubs., Dubuque, IA. 214 pp.

_____ and Y. JUNG. 1988. Land snails of the University of Michigan Biological Station area. Walkerana Vol. 3, No. 9. 177 pp.

_____ and T. A. PIERCE. 1990. Terrestrial gastropoda. Pages 201-310 *in* D. Dindal (ed.) Soil Biology Guide. John Wiley & Sons, Inc., New York, NY.

CLARKE, A. H., J. P. KELSALL, and G. R. PARKER. 1968. The landsnail fauna of Fundy National Park, New Brunswick. Bull. Nat. Mus. Can., No. 223. 22 pp.

DEGIUSTI, D. L. 1955. The occurrence of a protostrongylid nematode in the meninges of Michigan deer. J. Parasitol. 41(2):42 (abstr.).

_____. 1963. Incidence and distribution of *Elaphostrongylus odocoilei* in Michigan deer herd. J. Parasitol. 49 (Suppl.): 47.

DEW, T. L. 1988. Prevalence of *Parelaphostrongylus tenuis* in a sample of hunter-harvested white-tailed deer from a tri-county area in northeastern Wisconsin. J. Wildl. Diseases 24:720-721.

DIKMANS, G. 1935. Lungworms collected from deer, *Odocoileus virginianus*, in Michigan. Proc. Helminthol. Soc. Wash. 2: 59 (abstr.).

FORRESTER, S. G. and M. W. LANKESTER. 1998. Over-winter survival of first-stage larvae of *Parelaphostrongylus tenuis* (Nematoda: Protostrongylidae). Can. J. Zool. 76:704-710.

GETZ, L. L. 1974. Species diversity of terrestrial snails in the Great Smoky Mountains. The Nautilus 88: 6-9.

_____ and L.F. CHICHESTER. 1971. Introduced European slugs. The Biologist 53:118-127.

GLEICH, J. G. and F. F. GILBERT. 1976. A survey of terrestrial gastropods from central Maine. Can. J. Zool. 54:620-627.

GRAY, J. B., W. M. SAMUEL, A. W. SHOSTAK, and M. J. PYBUS. 1985. *Varestrongylus alpenae* (Nematoda: Metastrongyloidea) in white-tailed deer (*Odocoileus virginianus*) of Saskatchewan. Can. J. Zool. 63:1449-1454.

HILL, H. R. 1994. The 1994 deer pellet group surveys. Mich. Dep. Nat. Resour., Wildl. Div., Rep. No. 3211. 15 pp.

KARNS, P. D. 1967. *Parelaphostrongylus tenuis* in deer in Minnesota and implications for moose. J. Wildl. Manage. 31:299-303.

KEARNEY, S. R. and F. F. GILBERT. 1978. Terrestrial gastropods from the

Himsworth Game Preserve, Ontario, and their significance in *Parelaphostrongylus tenuis* transmission. Can. J. Zool. 56:688-694.

LANKESTER, M. W. and R. C. ANDERSON. 1968. Gastropods as intermediate hosts of *Pneumostrongylus tenuis* Dougherty of white-tailed deer. Can. J. Zool. 46:373-383.

_____ and W. J. PETERSON. 1996. The possible importance of wintering yards in the transmission of *Parelaphostrongylus tenuis* to white-tailed deer and moose. J. Wildl. Diseases 32:31-38.

_____ and W.M. SAMUEL. 1998. Pests, parasites and diseases. Pages 479 - 517 *in* A. W. Franzmann and C. C. Schwartz (eds.) Ecology and management of the North American moose. Smithsonian Inst. Press, Washington, DC.

LATCHFORD, F. R. 1885. Observations on the terrestrial mollusca of Ottawa and vicinity. Trans. Ottawa Field-Nat. Club 2:211-231.

LEE, C. B. 1952. Ecological aspects of *Stenotrema hirsutum* (Say) in the region of Ann Arbor, Michigan. Am. Midl. Nat. 47:55-60.

LEONG, T. S. and J. C. HOLMES. 1981. Communities of metazoan parasites in open water fishes of Cold Lake, Alberta. J. Fish Biol. 18:693-713.

LOKEN, K. I., J. C. SCHLOTTHAUER, H. J. KURTZ, and P. D. KARNS. 1965. *Pneumostrongylus tenuis* in Minnesota moose (*Alces alces*). Bull. Wildl. Dis. Assoc. 1:7.

MARGOLIS, L., G. W. ESCH, J. C. HOLMES, A. M. KURIS, and G. A. SCHAD. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). J. Parasitol. 68:131-133.

MAZE, R. J. and C. JOHNSTONE. 1986. Gastropod intermediate hosts of the meningeal worm *Parelaphostrongylus tenuis* in Pennsylvania: observations on their ecology. Can. J. Zool. 64:185-188.

(MDNR) MICHIGAN DEPARTMENT OF NATURAL RESOURCES. 1996. Michigan deer population figures, 1938 - 1996. Unpubl. Rep., Wildl. Div., Lansing, MI. 1 p.

_____. 1997a. Moose mortalities examined at the lab 1985 to 1997. Unpubl. Rep., Wildl. Div., Lansing, MI. 3 pp.

_____. 1997b. The 1997 deer pellet group surveys. Unpubl. Rep., Wildl. Div., Lansing, MI. 1 p.

_____. 1997c. Result of moose census. Unpubl. Rep., Wildl. Div., Lansing, MI. 5 pp.

NEWCOMB, L. 1977. Newcomb's wildflower guide. Little, Brown and Co., Boston, MA. 490 pp.

PETERSON, W. J., M. W. LANKESTER, and M. R. RIGGS. 1996. Seasonal and annual changes in shedding of *Parelaphostrongylus tenuis* larvae by white-tailed deer in northeastern Minnesota. Alces 32:61-73.

PLATT, T. R. 1978. The life cycle and systematics of *Parelaphostrongylus odocoilei* (Nematoda: Metastrongyloidea), a parasite of mule deer (*Odocoileus hemionus hemionus*), with special reference to the molluscan intermediate host. Ph.D. Thesis, Univ. Alberta, Edmonton. 233 pp.

_____. 1989. Gastropod intermediate hosts of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) from northwestern Indiana. J. Parasitol. 75:519-523.

PRESTWOOD, A. K. 1972. *Parelaphostrongylus andersoni* sp. n. (Metastrongyloidea: Protostrongyloidea) from the musculature of white-tailed deer (*Odocoileus virginianus*).

J. Parasitol. 58:897-902.

_____ and J. F. SMITH. 1969. Distribution of meningeal worm (*Pneumostrongylus tenuis*) in deer in the southeastern United States. J. Parasitol. 55:720-725.

PRIOR, D. J. 1985. Water-regulatory behaviour in terrestrial gastropods. Biol. Res. 60:403-424.

PYBUS, M. J. and W. M. SAMUEL. 1984. *Parelaphostrongylus andersoni* (Nematoda: Protostrongylidae) and *P. odocoilei* in two cervid definitive hosts. J. Parasitol. 70:507-515.

_____, _____, D. A. WELCH, and C. J. WILKE. 1990. *Parelaphostrongylus andersoni* (Nematoda: Protostrongylidae) in white-tailed deer in Michigan. J. Wildl. Diseases 26:535-537.

RASKEVITZ, R. F., A. A. KOCAN, and J. H. SHAW. 1991. Gastropod availability and habitat utilization by wapiti and white-tailed deer sympatric on range enzootic for meningeal worm. J. Wildl. Diseases 27:92-101.

RENECKER, L. A. 1987. Bioenergetics and behavior of moose (*Alces alces*) in the aspen dominated boreal forest. Ph.D. Thesis, Univ. Alberta, Edmonton. 265 pp.

_____ and R. J. HUDSON. 1986. Seasonal foraging rates of free-ranging moose. J. Wildl. Manage. 50:143-147.

_____ and C. C. SCHWARTZ. 1998. Food habits and feeding behavior. Pages 403-439 *in* A. W. Franzmann and C. C. Schwartz (eds.) Ecology and management of the North American moose. Smithsonian Inst. Press, Washington, DC.

ROGERS, L. L. 1987. Seasonal changes in defecation rates of free-ranging white-tailed deer. J. Wildl. Manage. 51:330-333.

ROWLEY, M. A., E. S. LOKER, J. F. PAGELS, and R. J. MONTALI. 1987. Terrestrial gastropod hosts of *Parelaphostrongylus tenuis* at the National Zoological Park's Conservation and Research Center, Virginia. J. Parasitol. 73:1084-1089.

SAMUEL, W. M. and J. B. GRAY. 1982. Evaluation of the Baermann technique for recovery of lungworm (Nematoda: Protostrongylidae) larvae from wild ruminants. Bienn. Symp. Wild Sheep and Goat Counc. 3:232-243.

_____, T. R. PLATT, and S. M. KNISKEL-KRAUSE. 1985. Gastropod intermediate hosts and transmission of *Parelaphostrongylus odocoilei*, a muscle-inhabiting nematode of mule deer, *Odocoileus h. hemionus*, in Jasper National Park, Alberta. Can. J. Zool. 63:928-932.

_____ and D. O. TRAINER. 1969. A technique for survey of some helminth and protozoan infections of white-tailed deer. J. Wildl. Manage. 33:888- 94.

SCHMITT, S. M., H. R. HILL, and T. M. COOLEY. 1983. Upper Peninsula brainworm incidence survey - 1982. Mich. Dep. Nat. Resour., Wildl. Div., Rep. No. 2944. 6 pp.

_____, _____, and _____. 1987. Upper Peninsula brainworm incidence survey - 1987. Mich. Dep. Nat. Resour., Wildl. Div., Rep. No. 3059. 7 pp.

_____, _____, and _____. 1988. Upper Peninsula brainworm incidence survey - 1988. Mich. Dep. Nat. Resour., Wildl. Div., Rep. No. 3084. 9 pp.

_____, _____, and _____. 1989. Upper Peninsula brainworm incidence survey - 1989. Mich. Dep. Nat. Resour., Wildl. Div., Rep. No. 3108. 8 pp.

SEVERINGHAUS, C. W. 1949. Tooth development and wear as criteria of age in white-tailed deer. J. Wildl. Manage. 13:195-216.

SHOSTAK, A. W. and W. M. SAMUEL. 1984. Moisture and temperature ef-

fects on survival and infectivity of first-stage larvae of *Parelaphostrongylus odocoilei* and *P. tenuis* (Nematoda: Metastrongyloidea). J. Parasitol. 70:261-269.

SKINNER, W. R. and E. S. TELFER. 1974. Spring, summer, and fall foods of deer in New Brunswick. J. Wildl. Manage. 38:210-214.

SLOMKE, A. M., M. W. LANKESTER, and W. J. PETERSON. 1995. Infrapopulation dynamics of *Parelaphostrongylus tenuis* in white-tailed deer. J. Wildl. Diseases 31:125-135.

TER BRAAK, C. J. F. 1987a. CANOCO - a FORTRAN program for canonical community ordination by partial, detrended, canonical correspondence analysis, principal components analysis, and redundancy analysis (version 2.1). TNO Inst. Appl. Computer Sci., Wageningen, Netherlands. 92 pp.

_____. 1987b. The analysis of vegetation-environment relationships by canonical correspondence analysis. Vegetation 69:69-77.

UPSHALL, S. M., M. D. B. BURT, and T. G. DILWORTH. 1986. *Parelaphostrongylus tenuis* in New Brunswick: the parasite in terrestrial gastropods. J. Wildl. Diseases 22:582-585.

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

VERME, L. J. 1965. Swamp conifer deeryards in northern Michigan. J. For. 63:523-529.

VOSS, E. G. 1972. Michigan Flora, Part I Gymnosperms and Monocots. Cranbrook Inst. Sci., Bloomfield Hills, MI. 488 pp.

_____. 1985. Michigan Flora, Part II Dicots (Saururaceae - Cornaceae). Regents of the Univ. Mich., Ann Arbor, MI. 724 pp.

WALTON, M. L. 1963. Length of life in west American land snails. The Nautilus 76:127-131.

WASEL, S. M. 1995. Meningeal worm, *Parelaphostrongylus tenuis* (Nematoda), in Manitoba, Saskatchewan, and North Dakota: Distribution and ecological correlates. M.Sc. Thesis, Univ. Alberta, Edmonton. 100 pp.

WECKERLY, F. W. and M. L. KENNEDY. 1992. Examining hypotheses about feeding strategies of white-tailed deer. Can. J. Zool. 70:432-439.

WHITLAW, H. A., M. W. LANKESTER, and W. B. BALLARD. 1996. *Parelaphostrongylus tenuis* in terrestrial gastropods from white-tailed deer winter and summer range in northern New Brunswick. Alces 32:75-83.

ZAR, J. H. 1984. Biostatistical analysis. Second ed. Prentice-Hall, Inc., Englewood Cliffs, NJ. 718 pp.