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THE POSSIBLE IMPORTANCE OF WINTERING YARDS IN THE TRANSMISSION OF *PARELAPHOSTRONGYLUS TENUIS* TO WHITE-TAILED DEER AND MOOSE

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ABSTRACT: Terrestrial gastropods were collected, 15 June to 25 November 1994, from beneath cardboard sheets on deer range in northeastern Minnesota (USA) and examined individually for larvae of *Parelaphostrongylus tenuis*, the meningeal worm of white-tailed deer (*Odocoileus virginianus*). Overall, 10 (0.08%) of 12,096 snails and slugs were infected with a mean (±SD) of 3.2 ± 2.5 *P. tenuis* larvae. The prevalence of infection in gastropods was greater in a traditional deer wintering yard (seven of 4,401, 0.16%), where deer aggregated for almost 5 months at a density of 50/km^2, than on summer range (three of 7,695, 0.04%) where they occurred at 4/km^2. Despite relatively low densities of infected gastropods, their ingestion purely by chance remains a tenable explanation for the high prevalence of *P. tenuis* infection observed in white-tailed deer.

Key words: *Parelaphostrongylus tenuis*, white-tailed deer, *Odocoileus virginianus*, terrestrial gastropods, winter yards, moose.

INTRODUCTION

Near the northern limits of their range, white-tailed deer (*Odocoileus virginianus*) typically migrate varying distances in late fall to aggregate in traditional areas called yards. Here, mature softwood stands offer protection from deep snow (Verme and Ozoga, 1971) and interspersed openings and early successional vegetation provide browse to meet winter food requirements (Mautz, 1978). High densities of deer in wintering yards for 4 to 5 mo concentrate fecal material, as well as first-stage larvae of *P. tenuis* that can survive freezing (Lankester and Anderson, 1968). Yards may represent important foci of infection to white-tails, and also to moose (*Alces alces*) since yarding behavior is most pronounced in the more northerly extensions of deer range.

In the vicinity of Grand Marais, Minnesota (USA) (47°45′N, 90°30′W), whitetails migrate up to 30 km to spend the winter on south facing slopes within 1 to 3 km of Lake Superior. The Jonvik deer yard, a 10-km segment of this area, has been used by wintering deer since at least 1936. Densities were estimated to be 82 deer/km^2 in 1936 (Krefting, 1938) and 45/km^2 in the winter of 1972 (Peterson, 1973). Up to 82% of the wintering deer currently are infected with *P. tenuis* (Slomke et al., 1995). Moose density in northeastern Minnesota is estimated at 0.3/km^2 overall but is much lower in the study area near the shore of Lake Superior (Lenarz, 1993a)

Our purpose was to test the hypothesis that deer wintering yards will have greater densities of infected gastropods than will summer deer range, and yards therefore will have greater potential for transmission of *P. tenuis* to deer and moose that frequent them during snow-free seasons.

METHODS

The wintering habitat sampled was located 22 km southwest of Grand Marais, adjacent to Minnesota State Highway 61 (47°41′N, 90°35′W). Vegetation included residual white cedar (*Thuja occidentalis*) and white spruce (*Picea glauca*) that survived a blow-down in 1959, regenerating white birch (*Betula papyrifera*), white spruce with mountain maple (*Acer spicatum*), speckled alder (*Alnus rugosa*), red osier dogwood (*Cornus stolonifera*), and beaked hazel (*Corylus cornuta*).

The summer area sampled was 7 km north, northeast of the wintering yard. It had been scarified and replanted with white spruce 15 yr earlier but was never released using herbicide or tending. Competing vegetation included dense growths of willows (*Salix* spp.), white birch, mountain maple, pin cherry (*Prunus*

pennsylvanica), speckled alder, and beaked hazel.

Use of the yard by deer during the previous winter was estimated by counting pellet groups, 28 April to 7 May 1994, in 75 plots randomly selected on 50 transect lines spaced 40 m apart. Each 320 m^2 plot was comprised of four subplots (20 × 4 m) located at 45 degree angles to, and 2 m distant from, the main transect line. Pellet groups per hectare were converted to a density estimate using a defecation rate of 13 pellet groups per day (Peterson, 1973) and a residency time of 141 days (26 November 1993 to 15 April 1994). Deer density on the summer range sampled was estimated using the methods of Lenarz (1993b) and adjusted to reflect the higher than average habitat quality.

The cardboard sheet sampling method described by Lankester and Anderson (1968) was used to collect gastropods weekly from 15 June to 3 September, and biweekly until 25 November, 1994 (n = 18 sampling times). Unwaxed, corrugated cardboard sheets approximately 1 m^2 were placed 10 to 15 m apart along transects up to 400 m long; 100 sheets were placed along four transect lines in the wintering area and 100 along five lines in the summer area. Sheets were placed to the side of game trails and without reference to deer pellet groups. The cardboard sheets were weighted down with small rocks or logs to reduce moisture loss from beneath and to prevent their being blown away. Gastropods were collected during the first few hours after daybreak, since numbers found beneath the sheets declined toward midday, especially on warm, sunny days. The sheets were moved 1 to 3 m every 3 to 4 wk. Mean weekly temperatures for the wintering area were obtained from the National Weather Service records, Grand Marais Minnesota (USA) and for the summer area, at Poplar Lake, Minnesota, 34 km north of Grand Marais.

Snails and slugs were transferred from collecting jars into plastic containers with lids and placed on ice in a chest cooler before returning from the field. In the laboratory, gastropods were stored at 4 C in containers with moistened sheets of synthetic foam. When slugs were kept on moist paper towel, they consumed it and the paper fibers released following pepsin digestion made searching for larvae difficult.

Gastropods were identified with the aid of Burch (1962) and Pilsbry (1946, 1948). Most were digested individually, or in groups of two or three, in flat-bottomed, 4 cm diameter Petri dishes in about 3 ml of artificial pepsin solution composed of 1 g powdered pepsin and 1.3 ml concentrated hydrochloric acid in 166 ml of tap water (Lankester and Anderson, 1968). After about 16 hr at 35 to 40 C, the Petri dishes were examined for larvae under a stereoscopic microscope with sub-stage illumination at 16×. To systematically scan the contents of the dish, each was placed on a 8 × 8 cm piece of plate glass with a 75 mm etched grid. The glass plate slid more easily over the microscope stage when it was covered with a piece of lightweight polyethylene.

Two abundant slugs (*Arion circumscriptus* and *Deroceras reticulatum*) were digested in batches of up to 35 after sufficient numbers had been digested individually to establish that the frequency of infection was very low. Batches of slugs were suspended over a piece of vinyl window screening in a large, glass, stoppered funnel (top diameter 145 mm). Digestion and direct examination of gastropods individually, provides a measure of intensity of infection with all larval stages. In batch digests, first- and second-stage *P. tenuis* larvae die quickly in pepsin and cannot be detected; only third-stage larvae remain active and can be drained from Baermann funnels after 24 hr (Lankester and Anderson, 1968).

All nematodes found in gastropods were noted. Representative specimens were measured using a drawing tube and stage micrometer, and saved in 70% ethyl alcohol with 10% glycerin added. The identity of *P. tenuis* larvae was confirmed by comparing dimensions and morphological features to those illustrated by Anderson (1963). The distinctive C- or J-shape assumed by *P. tenuis* larvae when they die in pepsin digest or when they are heat-killed, also helped to distinguish them from some other nematodes in gastropods.

Data were analyzed in a 2 × 2 contingency table using Fisher's exact test (Agresti, 1990). Differences were considered significant at $P < 0.05$.

RESULTS

Ten (0.08%) of 12,096 gastropods were infected with *P. tenuis* (Table 1). The prevalence of infection was greater on the wintering area (seven of 4,401, 0.16%) than on the summer range (three of 7,695, 0.04%) (P = 0.04). Only five of 13 species collected were infected; four *Discus cronkhitei,* two *Deroceras laeve,* two *Deroceras reticulatum,* one *Succinea ovalis,* and one *Anguispira alternata.* Infected gastropods contained a mean (±SD) of 3.2 ± 2.5 (range one to seven) *P. tenuis* larvae. Three of four infected gastropods collected before 10 July contained first- or sec-

TABLE 1. Terrestrial gastropods with larvae of *Parelaphostrongylus tenuis* collected off winter and summer white-tailed deer range, Grand Marais, Minnesota, 15 June to 25 November 1994.

Gastropod species	Winter yard		Summer range		Total gastropods	Percent with *P. tenuis*
	Number examined[a]	Number with *P. tenuis*	Number examined[a]	Number with *P. tenuis*		
Deroceras laeve	515	0	697	2	1,212	0.17
D. reticulatum	1,757	2	5,192	0	6,949	0.03
Pallifera dorsalis	10	0	5	0	15	0.0
Arion circumscriptus[b]	302	0	843	0	1,145	0.0
A. subfuscus	0	0	1	0	1	0.0
Zonitoides arboreus	330	0	156	0	486	0.0
Discus cronkhitei	753	4	215	0	968	0.4
Succinea ovalis	330	0	63	1	393	0.3
Anguispira alternata	65	1	16	0	81	1.2
Euconulus fulvus	110	0	18	0	128	0.0
Cochlicopa lubrica	32	0	1	0	33	0.0
Zoogenetes harpa	53	0	59	0	112	0.0
Vitrina limpida	144	0	429	0	573	0.0
Total	4,401	7 (0.16)[c]	7,695	3 (0.04)	12,096	0.08

[a] Eighteen weekly or biweekly collections from beneath 100, 1 m^2 cardboard sheets in each area.
[b] Collection discontinued after 4 wk.
[c] Percent infected in parentheses.

ond-stage larvae. The six collected after this date (two each in July, September, and October) all contained third-stage larvae which were 1,075 ± 97 μm long (mean ± SD) (range 925 to 1210 μm, n = 15).

Larval and adult stages of nematodes other than *P. tenuis* were found in 448 (3.7%) of 12,096 gastropods examined. Some of these were similar in size to first- and third-stage larvae of *P. tenuis* and could be distinguished only after careful microscopic examination. *Discus cronkhitei, Zonitoides arboreus, Deroceras laeve,* and *Deroceras reticulatum* were the most frequently infected with larvae that could be confused with those of *P. tenuis.*

The density of gastropods found beneath cardboard sheets was almost twice as great in the summer area (4.3/m^2) as in the winter area (2.4/m^2) (Table 1). Total numbers of 12 gastropod species varied considerably over the sampling period (Fig. 1). For example, *Deroceras laeve, Discus cronkhitei,* and *Z. arboreus* were most abundant in early summer and in the fall with lower numbers in August. *Succinea ovalis* and *A. alternata* were most abundant in early summer while the numbers of *Vitrina limpida, Euconulus fulvus,* and *Zoogenetes harpa* increased toward late summer and fall. By casual observation in the laboratory, the most mobile species were *Deroceras reticulatum, Deroceras laeve,* and *V. limpida.*

The fall of 1994 was unusually warm and small numbers of gastropods could be collected as late as 25 November. Most species declined in numbers by the end of September but *Deroceras laeve, V. limpida, Discus cronkhitei,* and *E. fulvus* remained relatively numerous until mean, weekly, overnight low temperatures dropped below about 1.0 C. This occurred in the wintering area in the first week of November and in the summer area, a week earlier. A few *Deroceras laeve* and *V. limpida* still could be found beneath cardboard sheets when mean weekly overnight air temperature fell below zero (−0.6 to −2.7 C) but daytime highs were 1.9 to 2.9 C.

Based on an estimated deposition of 910 fecal groups per hectare, 13 groups per deer per day, for a period of 141 days, deer

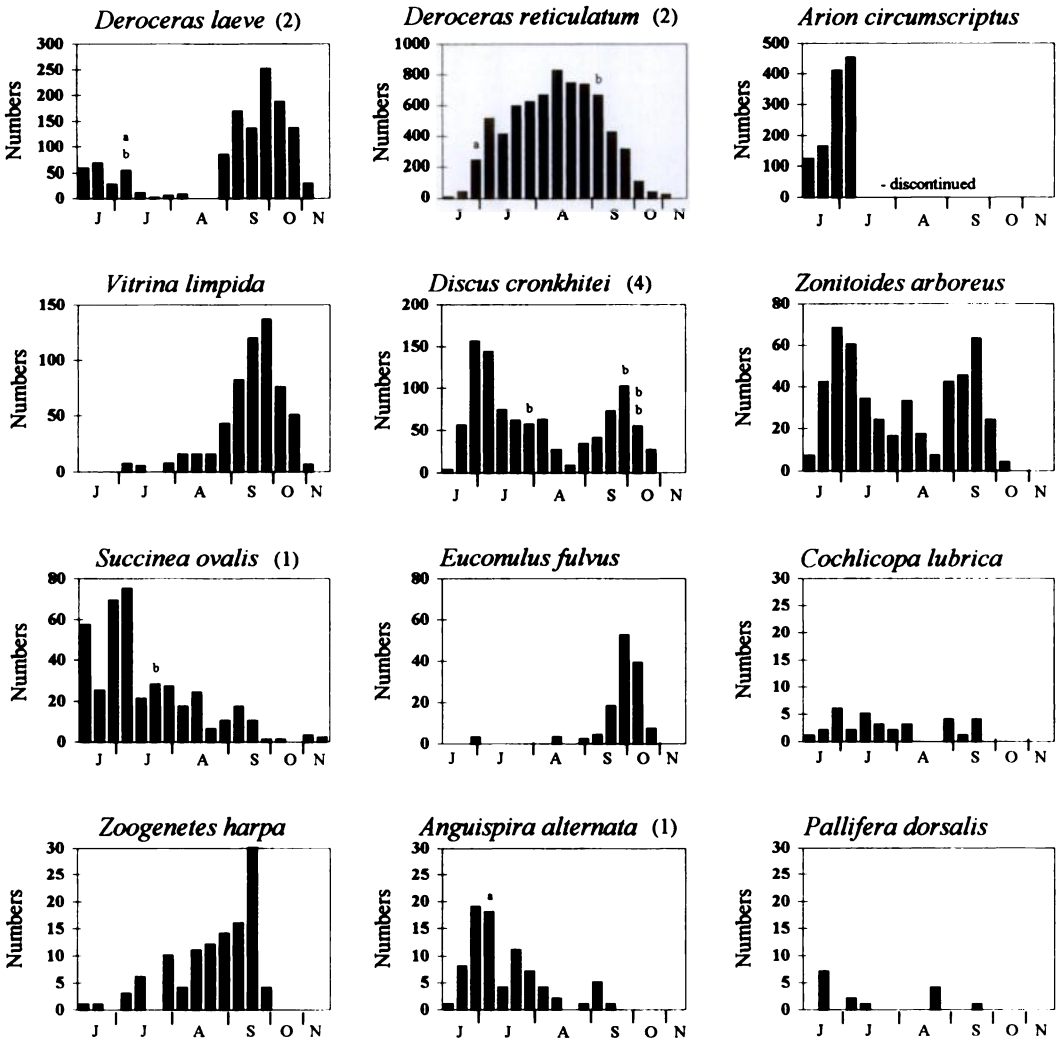

FIGURE 1. Twelve species of terrestrial gastropods collected from beneath 200 cardboard sheets from 15 June to 25 November 1994, near Grand Marais, Minnesota. Numbers of each species infected with *Parelaphostrongylus tenuis* are in brackets. Those gastropods containing first- or second-stage *P. tenuis* larvae are indicated by [a]; those with third-stage larvae by [b]. Letters on x-axis refer to June (J), July (J), August (A), September (S), October (O), and November (N).

density in the wintering area for 1993 to 1994 was estimated at 50/km^2. Deer were absent in the summer area from late November to mid-April; during this time almost all were aggregated in the winter yarding area. Deer density during summer, in both the winter and summer areas, was estimated at 4/km^2.

DISCUSSION

The potential for a deer or moose to become infected with *P. tenuis* was twice as great in the Jonvik winter deer yard as on summer range (seven and three infected gastropods found, respectively, in equal areas sampled). However, despite infected gastropods being able to survive winter (Lankester and Anderson, 1968), they may not be accessible to deer during this period. In most years, air temperatures were below 0 C and snow covered the ground by the time migrating deer arrived in the yard (W. J. Peterson, unpubl.). Although

deer in northeastern Minnesota can be seen in early winter (December) pawing through snow and eating vegetation off the ground (W. J. Peterson, unpubl.), it is not known which, if any, terrestrial gastropods remain in the superficial litter layer over winter.

The next opportunity for deer to ingest gastropods while still in the yarding area probably occurred from mid-March to mid-April, when snow began to melt. Patches of vegetation became exposed on south-facing slopes and under conifer trees where accumulation was shallow. Deer were attracted to these sites and relied heavily on them for 2 to 3 wk before dispersing. Daytime, ground temperatures often were high enough to thaw the litter layer and for gastropods such as *Deroceras laeve* to become active. However, even if infected gastropods were available and eaten in the yard, their contribution to infection of the deer herd at this time probably was limited. Slomke et al. (1995) demonstrated that up to 79% of fawns in northeastern Minnesota became infected with *P. tenuis* during their first summer and fall, before they moved into the winter yard. Also, since *P. tenuis* appears to be a long-lived parasite and accumulation of worms is limited by an immune response (Slomke et al., 1995), most of the deer in the yard in early spring already have acquired the worms they will have for a number of years.

Nonetheless, winter deer yards will present an increased risk of transmission to deer fawns born in the area and to moose present during the snow-free period. Moose are not as abundant near Lake Superior, Minnesota, as they are further inland in northeastern Minnesota but animals with signs of moose sickness are not infrequent. Twelve (43%) of 28 moose with confirmed parelaphostrongylosis in northeastern Minnesota over the past 23 years were observed along a 78-km length of the deer wintering area, within 1 km of the shoreline of Lake Superior (M. W. Lankester and W. J. Peterson, unpubl.). Moose in other areas, such as northern New Hampshire (USA), regularly forage in and around deer yards, particularly in autumn (Pruss and Pekins, 1992).

In our study, all *P. tenuis* larvae found in snails from July to October had reached the infective third stage, while most larvae in infected snails sampled earlier were pre-infective (first and second stage). Therefore, those gastropods known to harbor *P. tenuis* larvae and to remain abundant and active toward the end of summer will play the greatest role in transmission. In the Grand Marais area, this included, in decreasing order of importance, *Discus cronkhitei, Deroceras laeve, Deroceras reticulatum, S. ovalis,* and *A. alternata. Arion circumscriptus* was a very abundant slug. Although it can be infected with *P. tenuis,* it was not considered a particularly good intermediate host (Lankester and Anderson, 1968). Therefore, collection of *A. circumscriptus* was discontinued after the first week in July to prevent it from dominating the sample.

The mean (±SD) intensity of *P. tenuis* infection found in gastropods in this study (3.2 ± 2.5) was comparable to means of two to six larvae per infected gastropod as reported by Lankester and Anderson (1968), Gleich et al. (1977), and Upshall et al. (1986). In three separate reports, individual specimens of the slug *Deroceras laeve* have contained unusually large numbers of *P. tenuis* larvae; 97, 75, and 26 larvae reported, respectively, by Lankester and Anderson (1968), Maze and Johnstone (1986), and Platt (1989). Thus *Deroceras laeve* may be more likely than other species to be attracted to fresh deer feces rather than encountering *P. tenuis* larvae on dried feces or dispersed in the soil.

The overall prevalence at 0.08% found here in gastropods was similar to that reported in Maine (USA) at 0.1% (Gleich et al., 1977); in Algonquin Park, Ontario, Canada, at 1.0% (Lankester, 1967), near North Bay, Ontario at up to 0.12% (Kearney and Gilbert, 1978); and in northern Minnesota at 0.8% (Pitt and Jordan, 1995)

but is somewhat lower than that found in other areas. The higher prevalences reported on Navy Island, Ontario, at 4.2% (Lankester and Anderson, 1968), north-central Pennsylvania (USA) at 9.0% (Maze and Johnstone, 1986), and eastern Oklahoma (USA) at 8.0% (Raskevitz et al., 1991) probably were influenced mostly by the high deer densities in those study sites. Prevalence in Virginia (USA) at 2.2% (Rowley et al., 1987) and Indiana (USA) at 1.9% (Platt, 1989) may reflect high deer density, but also a warmer climate and longer season for gastropod activity. Similar prevalences were reported in the Canadian maritime provinces of Nova Scotia at 2.6% (Parker, 1966); New Brunswick at 2.0 to 2.5% (Beach, 1992; Upshall et al., 1986, respectively).

Although *Triodopsis* spp. did not occur in northeastern Minnesota, others have found an unusually high prevalence of *P. tenuis* (9.5% to 33%) in this snail (Lankester, 1967; Maze and Johnstone, 1986; Rowley et al., 1987; Raskevitz et al., 1991; Beach, 1992). Whether deer intentionally eat large snails such as these for additional protein, or possibly mistake them for mast, should be investigated.

The prevalence of *P. tenuis* larvae in terrestrial gastropods is dependent upon several factors. These include the density and residence time of infected deer, their defecation rates in particular areas, the survivorship of first-stage larvae on feces or dispersed in soil, and the abundance and mobility of suitable gastropods. Some or all of these factors probably account for foci of high prevalence in gastropods found by a few authors in particular microhabitats (Lankester and Anderson, 1968; Maze and Johnstone, 1986). However, areas with a high prevalence of infection in gastropods cannot be presumed to have greater importance in the transmission of *P. tenuis* without knowing the age and susceptibility of deer feeding there and to what extent they feed low to the ground when infected gastropods are available. As well, areas with permanent high density deer populations can be expected to have a high prevalence of infected gastropods, but because deer appear to have an upper threshold level of infection (Slomke et al., 1995), little of this increased potential for transmission may be realized. Slomke et al. (1995) found that deer confined year-round in an area at a density of 30/km^2 had the same number of adult *P. tenuis* in the cranium as deer existing at summer densities of 2/km^2 (mean ±SD of 3.5 ± 1.8 and 3.2 ± 2.2, respectively).

Anderson and Prestwood (1981) suggested that a high prevalence of infection in deer can occur despite a low prevalence of infected gastropods because of the large amount of vegetation consumed by these cervids. However, whether high food volume can explain the rapid infection of a large proportion of the fawn cohort, and whether ingestion of gastropods is purely accidental, are worth examining.

Deer fawns in the Grand Marais area reach a mean weight of 44 kg in the September to November period (W. J. Peterson, unpubl.); they are estimated to eat 1100 g dry weight of vegetation per day, based on a daily dry weight food requirement of 62.5 g per kg of body weight$^{3/4}$ (Huot, 1982). During autumn, 80% of this food (880 g/day) can be taken close to the ground from the grass-forb layer (Huot, 1982). Using the mean (±SD) dried weight of fallen white birch leaves at 76 ± 15 g/m^2 (M. W. Lankester and W. J. Peterson, unpubl.), this daily food requirement could be represented by a single layer of leaves covering an area of 11.6 m^2. On summer range, leaves covering this area had 50 terrestrial gastropods (4.3/m^2). If this much ground vegetation was eaten by a fawn for 51 days, in all liklihood it would ingest one infected gastropod (one of 2565 infected on summer range). Each infected gastropod had a mean (±SD) of 3.2 ± 2.5 larvae, similar to the mean number of adult worms acquired by fawns in this area before their first winter (2.8 ± 1.8) (Slomke et al., 1995). Therefore, the

accidental ingestion of infected gastropods distributed at random, even at the low frequency of infection found in our study, remains a feasible explanation for the high prevalence of *P. tenuis* in fawns by late autumn.

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LITERATURE CITED

AGRESTI, A. 1990. Categorical data analysis. John Wiley and Sons, New York, New York, 558 pp.

ANDERSON, R. C. 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. Canadian Journal of Zoology 41: 775–802.

———, AND A. K. PRESTWOOD. 1981. Lungworms. *In* Diseases and parasites of white-tailed deer, W. R. Davidson, F. A. Hayes, V. F. Nettles, and F. E. Kellogg (eds.). Miscellaneous Publications Number 7, Tall Timbers Research Station, Tallahassee, Florida, pp. 266–317.

BEACH, T. D. 1992. Transmission of meningeal worm: An analysis of sympatric use of habitat by white-tailed deer, moose and gastropods. M.Sc. Thesis. University of New Brunswick, Fredericton, New Brunswick, Canada, 214 pp.

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

GLEICH, J. G., F. F. GILBERT, AND N. P. KUTSCHA. 1977. Nematodes in terrestrial gastropods from central Maine. Journal of Wildlife Diseases 13: 43–46.

HUOT, J. 1982. Body condition and food resources of white-tailed deer on Anticosti Island, Quebec. Ph.D. Thesis. University of Alaska, Fairbanks, Alaska, 240 pp.

KEARNEY, S. R., AND F. F. GILBERT. 1978. Terrestrial gastropods from the Himsworth Game Preserve, Ontario, and their significance in *Parelaphostrongylus tenuis* transmission. Canadian Journal of Zoology 56: 688–694.

KREFTING, L. W. 1938. Deer management studies with special reference to methods of measuring browse. M.Sc. Thesis. University of Minnesota, Minneapolis, Minnesota, 75 pp.

LANKESTER, M. W. 1967. Gastropods as intermediate hosts of *Pneumostrongylus tenuis* Dougherty, of white-tailed deer. M.Sc. Thesis. University of Guelph, Guelph, Ontario, 67 pp.

———, AND R. C. ANDERSON. 1968. Gastropods as intermediate hosts of meningeal worm, *Pneumostrongylus tenuis,* Dougherty. Canadian Journal of Zoology 46: 373–383.

LENARZ, M. S. 1993a. Aerial moose survey results 1992–93. Unpublished report, Minnesota Department of Natural Resources, Grand Rapids, Minnesota, 6 pp.

———. 1993b. The white-tailed deer of Minnesota's forested zone: Harvest, population trends, and modeling. Unpublished report, Minnesota Department of Natural Resources, Grand Rapids, Minnesota, 9 pp.

MAUTZ, W. W. 1978. Sledding on a bushy hillside: The fat cycle in deer. Wildlife Society Bulletin 6: 88–90.

MAZE, R. J., AND C. JOHNSTONE. 1986. Gastropod intermediate hosts of the meningeal worm *Parelaphostrongylus tenuis* in Pennsylvania: Observations on their ecology. Canadian Journal of Zoology 64: 185–188.

PARKER, G. R. 1966. Moose disease in Nova Scotia. M.Sc. Thesis. Acadia University Wolfville, Nova Scotia, Canada, 126 pp.

PETERSON, W. J. 1973. Jonvik pellet count results. Unpublished report, Minnesota Department of Natural Resources, Area Wildlife Office, Grand Marais, Minnesota, 4 pp.

PILSBRY, H. A. 1946. Land mollusca of North America (north of Mexico). Monograph 3, Vol. II, Part 1. Academy of Natural Sciences, Philadelphia, Pennsylvania, 520 pp.

———. 1948. Land mollusca of North America (north of Mexico). Monograph 3, Vol II, Pt. 2. Academy of Natural Sciences, Philadelphia, Pennsylvania, 1,113 pp.

PITT, W. C., AND P. A. JORDAN. 1995. A survey of the nematode parasite *Parelaphostrongylus tenuis* in the white-tailed deer, *Odocoileus virginianus,* in a region proposed for caribou, *Rangifer tarandus caribou,* re-introduction in Minnesota. Canadian Field-Naturalist 108: 341–346.

PLATT, T. R. 1989. Gastropod intermediate hosts of *Parelaphostrongylus tenuis* (Nematoda: Metastrongyloidea) from northwestern Indiana. The Journal of Parasitology 75: 519–523.

PRUSS, M. T., AND P. J. PEKINS. 1992. Effects of moose foraging on browse availability in New Hampshire deer yards. Alces 28: 123–136.

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. Journal of Wildlife Diseases 27: 92–101.

ROWLEY, M. A., E. S. LOKER, J. F. PAGELS, AND R. J. MONTALL. 1987. Terrestrial gastropod hosts of *Parelaphostrongylus tenuis* at the National

Zoological Park's Conservation and Research Center. The Journal of Parasitology 73: 1084–1089.

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

UPSHALL, S. M., M. D. B. BURT, AND T. G. DILWORTH. 1986. *Parelaphostrongylus tenuis* in New Brunswick: The parasite in terrestrial gastropods. Journal of Wildlife Diseases 22: 582–585.

VERME, L. J., AND OZOGA. 1971. Influence of winter weather on white-tailed deer in upper Michigan. *In* Proceedings of the snow and ice in relation to wildlife and recreation symposium, A. O. Haugen (ed.). Iowa Cooperative Wildlife Research Unit, Iowa State University, Ames, Iowa, pp. 16–28.

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