ASPECTS OF THE EPIZOOTIOLOGY OF *PARELAPHOSTRONGYLUS TENUIS* IN A WHITE-TAILED DEER POPULATION

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ABSTRACT: Larvae of *Parelaphostrongylus tenuis* occurred in 44% of fecal samples from 832 known-age white-tailed deer (*Odocoileus virginianus*) killed by vehicles October, 1986 to September 1990 in northeastern Minnesota. The earliest a fawn was found passing larvae was 12 October. Prevalence of larvae in feces of fawns rose steadily through autumn and winter (Sept.-Feb.). Forty-six percent were passing larvae by the time they approached one year of age and 68% at 12-15 mth. The overall prevalence in deer older than one yr, was 58% and it did not vary with increasing age. Prevalence of larvae in feces varied between years (32%, 45%, 44%, 52% in 1986-90, respectively) and with season; more deer passed larvae in spring (67%) than in autumn and winter (49 and 53%). Changes in prevalence were likely due to climatological factors affecting transmission from gastropods and not to changes in deer density. The mean number of larvae in feces was positively skewed ($\bar{X}$=51.7+6.1/g fresh feces; range = 1-1250/g) and negatively correlated with age; fawns and yearlings passed the most. More larvae were passed in spring by deer of all ages than at other times of the year.

The prevalence of *P. tenuis* in a deer herd is seen as an easily measured yet comprehensive index of the many host and habitat factors that interact to determine the overall success of the parasite . As such, it may also be the best measure of the risk of *P. tenuis* being transmitted to sympatric moose. Prevalence measured by examining deer heads for adult worms will differ from that determined by examining feces for larvae.

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The meningeal worm, *Parelaphostrongylus tenuis*, occurs commonly in white-tailed deer (*Odocoileus virginianus*) over much of their range in eastern North America (see review by Anderson and Prestwood 1981). This nematode causes a severe neurologic disease in moose (*Alces alces*) and other native cervids where they share habitat with infected white- tails (Anderson 1964, 1972). Despite the recognized importance of this parasite in the management, movement and husbandry of cervids, much remains to be known about its biology and transmission within populations of the normal host, white-tailed deer (Lankester 1987).

A high road-kill area in northeastern Minnesota provided an opportunity to collect fecal samples from white-tailed deer of known age throughout a number of consecutive years. Vehicles travelling Highway 61 kill several hundred deer each year in a narrow strip of land (2-3 km wide and 180 km long) along Minnesota's north shore of Lake Superior. The area is the traditional wintering location for deer whose summer ranges occur up to 20 or more km inland. Most deer are killed between October and April but some deer remain after winter aggregations disperse and these resident animals comprise the sample during the rest of the year.

In this study, feces from aged, vehicle-killed deer were examined using the Baermann technique in an attempt to learn more about those factors that influence the prevalence and numbers of first-stage *P. tenuis* larvae shed by white-tailed deer.

METHODS

Fecal samples were collected from the colons of 832 white-tailed deer killed by vehicles from October 1986 through September 1990. Samples were frozen at -16^{0}C for up to

one month before being examined for nematode larvae using the Baermann technique. Samples were thawed and weighed and larvae were extracted from 15-25 g of feces placed over a single layer of tissue paper (Kimberly-Clark Kimwipes) in a glass funnel (90 mm top diam.) filled with water. After 24 h, 12 to 15 ml of sediment were drained from the funnel into a Syracuse watch glass (54 mm diam.) with a grid etched on the bottom. Larvae were counted and expressed as numbers of larvae per g of fresh feces (lpg).

Deer are assumed to have been born June 1. Ages were determined from eruption and replacement of teeth and by counting cementum annuli. Data were analyzed using 4 age classes: fawns (age <1 yr, collected June 1 through to May 31); yearlings (age 1 yr, in their 2nd year of life); and 2 grouped age classes of adult deer (ages 2-6 and 7-16 yr). The regression of numbers of larvae in feces on age was done using 17 individual age classes. Analyses of seasonal differences were done by pooling collection data according to summer (June-Aug.), autumn (Sept.-Nov.), winter (Dec.-Feb.), and spring (Mar.-May).

Statistical analyses included standard univariate contingency Chi-square (χ^2) tests to detect differences in prevalence (percentage of deer passing larvae). A multivariate analysis of covariance was used to assess effects of year, season, sex and age on the natural logarithm (ln) of the mean numbers of larvae per g of fresh fecal samples. Also, pairwise t-tests were used to compare means of individual seasons within, and across, age classes.

In this study, all recovered dorsal-spined nematode larvae were assumed to be those of *P. tenuis*. Adult *P. tenuis* were found in 40 heads of deer passing larvae and dimensions of larvae in feces were similar to those published for this species (Anderson 1963). Also, about half of the deer examined from central and northern Minnesota by Karns (1967, 1977) had adult *P. tenuis* in the cranium. *Parelaphostrongylus andersoni*, which occurs sporadically in white-tailed deer (Prestwood 1972, Pybus and Samuel 1981, Pybus *et al.* 1990) was not found on examining one longissimus dorsi muscle from each of a subsample of 35 deer. *Varestrongylus alpenae*, a lungworm with especially short larvae (Gray *et al.* 1985), is not believed to have been present.

RESULTS

Forty-four percent of a total of 832 white-tailed deer fecal samples contained larvae of *Parelaphostrongylus tenuis* (Table 1). The prevalence of larvae in the feces of fawns (27%) was lower than that in the older age classes (overall = 58%; yearlings = 57%; 2-6 yr = 60%; 7-16 yr = 57%)($P<0.001$) but prevalence did not differ between older age classes.

The earliest patent infections in fawns were found on October 12 and 30; no others were noted until mid-December. The prevalence of larvae in feces of fawns continued to increase through winter and spring and, in the second summer of life reached 68% (Fig. 1). Prevalence did not vary with season when the 3 older age classes were analyzed individually. However, because prevalence by season was similar among the 3 age classes, data were pooled. Then prevalence in spring (67%) was greater than in autumn (49%) ($P=0.01$) and winter (53%) ($P=0.01$) but not different from that in summer (64%) (Fig. 2).

Prevalence in fawns did not vary significantly from year to year (summer of 1990 excluded because of small sample)(Fig. 3). In pooled yearlings and adults, however, prevalence was lower in 1986-87 (40%) than in the 3 succeeding years (64%, 58%, 65% respectively)($P<0.01$), which were not different from each other. In particular, the prevalence in yearlings examined in 1986-87 (32%) was significantly lower than in yearlings for the next three years (also 64%, 58%, 65%, respectively)($P<0.01$).

Table 1. Seasonal prevalence and mean number of *Parelaphostrongylus tenuis* larvae per gram of white-tailed deer feces collected in northeastern Minnesota, Oct. 1986 - Sept. 1990.

Deer Age Class	Season	Prevalence %	Prevalence n	Number of Larvae / g Mean	SE	Mean ln	SE
	Summer	-	9	-	-	-	-
	Autumn	3 a*	75	0.7	0.62	-1.37 j	1.63
<1	Winter	26 a,b	193	35.4	9.01	1.67 k	0.37
	Spring	46 b,c,d,e	115	121.0	24.90	3.57 j,k,l	0.28
	Sub-Total	27 g,h,i	392	77.5	15.33	2.56 w,x	0.25
	Summer	68 c	34	40.8	17.34	2.80 m,n,o	0.27
	Autumn	47	34	29.3	11.27	1.65 m	0.67
1	Winter	53	49	32.8	9.97	1.61	0.51
	Spring	61	56	77.8	15.72	2.92 p	0.44
	Sub-Total	57 g	173	49.6	7.65	2.34 y	0.24
	Summer	62	21	5.3	1.80	0.54 n,p,q	0.51
	Autumn	52	23	20.7	10.21	0.85 r	0.77
2-6	Winter	53 f	96	33.2	7.80	1.74	0.34
	Spring	72 f,d	60	62.1	13.52	2.68 l,q,r,s	0.36
	Sub-Total	60 h	200	39.3	6.22	1.86 w	0.22
	Summer	50	6	0.5	0.37	-1.47 o,s,t,u	0.83
	Autumn	46	11	12.7	10.31	0.32	1.34
7-16	Winter	54	35	11.3	5.36	1.02 t,v	0.44
	Spring	73 e	15	56.1	22.35	2.80 u,v	0.57
	Sub-Total	57 i	67	23.6	7.71	1.25 x,y	0.37
Total		44	832	51.7	6.11	2.13	0.13

* Values followed by the same letter were significantly different ($P \leq 0.05$).

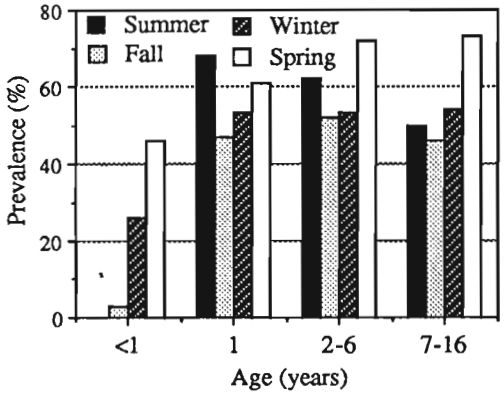
Prevalence was lower in males (38 %) than in females (47%) only when all data were pooled (P=0.01) but this should probably be discounted because of sampling bias. Sixty-eight percent of the males sampled were fawns, the age class least infected. Whereas, only 35% of the females were fawns.

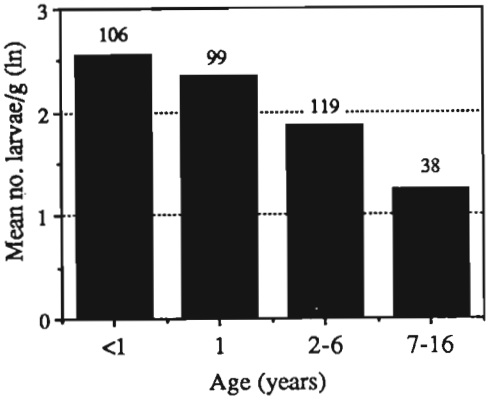
The number of larvae per gram of feces ranged from less than 1 to 1250 ($\bar{x}$=51.7+6.1). Because data were highly skewed (20% of samples had less than 1 lpg and 45% had less than 10 lpg), they were converted to natural logarithms (ln).

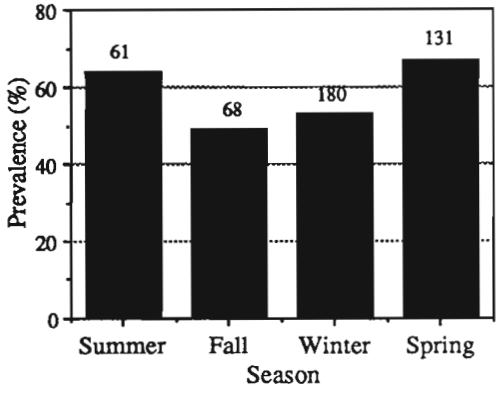
The number of larvae per g (ln) was negatively correlated with increasing age of deer (17 age classes)(r=-0.19, P<0.001). The mean number of larvae per g (ln) was greater in fawns than in adults 2-6 yr (P=0.04) and adults 7-16 yr (P=0.01) and the mean number of larvae per g (ln) in yearlings was greater than that in adults 7-16 yr (P=0.02) (Fig. 4).

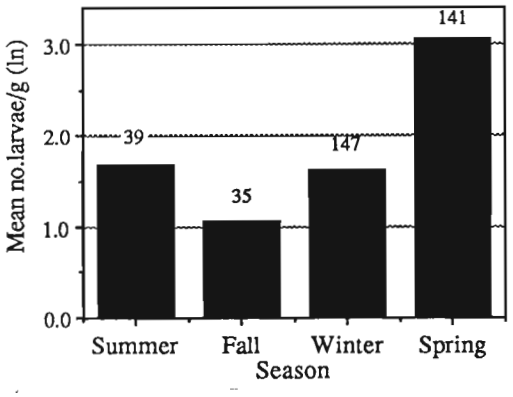
After adjusting for a significant age effect (P=0.01), analysis of covariance revealed that the mean number of larvae per g of feces (ln) varied with season (P<0.001) and was greater in spring than in summer (P<0.01), autumn (P<0.001), or winter (P<0.001)(least square means tests on age-adjusted seasonal means (Neter *et al.* 1985) (Fig. 5). The greatest mean numbers of larvae were passed in the spring (Mar.-May) by all age classes (Table 1.). Only yearling animals (12-15 mth old) came close to passing such high numbers of larvae during summer.

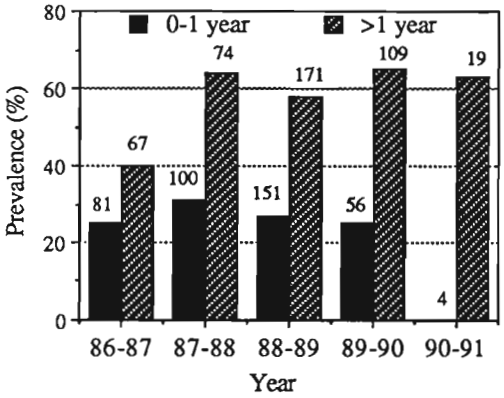
Climatological data recorded at Grand Marais, MN for the period 1980-91 are given in Table 2.











Figs. 1-3. Prevalence of first-stage *Parelaphostrongylus tenuis* larvae in feces of white- tailed deer killed by vehicles in northeastern Minnesota. Fig. 1. Differences in prevalence in relation to age and season in which deer were collected. Fig. 2. Differences in prevalence in yearling and adult deer (pooled) in relation to season. Fig. 3. Annual differences in prevalence in fawns and older deer. Vertical bars are subtended by sample sizes.

Figs. 4-5. Mean numbers of *P. tenuis* larvae (expressed as natural logarithms) per g of fresh feces from white-tailed deer killed by vehicles in northeastern Minnesota. Fig. 4. Mean numbers of larvae (ln) passed by deer of different age. Fig. 5. Mean numbers of larvae (ln) passed at different times of the year.

DISCUSSION

In order to interpret data presented here on the prevalence and numbers of *P. tenuis* larvae passed by deer, it may be useful to review some pertinent aspects of the parasite's life cycle. First-stage larvae of *P. tenuis* are in the film of mucous covering fecal pellets passed by infected deer (Lankester and Anderson 1968). Larvae resist freezing for long periods but their presumed resistance to drying and direct solar radiation is less well studied. Terrestrial snails and slugs, which are the required intermediate hosts, become

Table 2. Meteorological data for Grand Marais, MN, 1980-91.

Year	Snow-free Days	Precipitation* (cm)	Temperature* (°C)
1980	210	32.8	13.7
81	238	29.1	13.2
82	196	32.6	12.0
83	203	26.2	13.2
84	245	24.3	13.2
85	217	35.7	12.4
86	217	39.0	13.0
87	237	41.5	14.7
88	238	42.8	14.8
89	201	34.6	12.5
90	241	25.9	12.9
91	209	22.9	13.3
12 Year Mean	221.0	32.3	13.2

*May-August period.

infected with first-stage larvae when they crawl over deer feces or encounter larvae that have been washed by rain into the soil. Important slugs such as *Deroceras laeve* have been studied in temperate areas (Getz 1959, Lankester and Anderson 1968) but little is known about the seasonal movements of snails and slugs at more northern latitudes or about where they spend winter. Infection of gastropods occurs at the greatest rate during wet periods, especially spring. However, infection occurs throughout summer and fall, particularly in habitats that retain moisture. Larvae develop to the infective stage in gastropods in 3-5 weeks at 20°C but probably require longer at lower and fluctuating field temperatures; development stops when snails estivate. Infective *P. tenuis* larvae survive in gastropods over winter (Lankester and Anderson 1968).

Deer become infected when they accidentally ingest gastropods with vegetation. It is assumed that infection is improbable or rare over winter when soil and litter are frozen and snow-covered. About three months are required for adult worms to mature in the cranium and for first-stage larvae to appear in feces (Anderson 1963). The course of *P. tenuis* larval output following patency has not been studied closely but larval production of related species increases rapidly to a peak in 2-5 weeks and then slowly declines to lower levels (Platt and Samuel 1978, Pybus and Samuel 1984). The life span of adult *P. tenuis* in the cranium is not known but they may live 6 or more years as does *Elaphostrongylus cervi*, a close relative (Watson 1984). The intensity of infection (number of worms per infected deer) varies from about 1-9 and infected deer appear to acquire a degree of immunity that limits repeated and heavy infection (Anderson and Prestwood 1981).

Lankester (1987) emphasized the value of prevalence data for *P. tenuis* as an easily measured index reflecting the overall success of the parasite in reaching its final host under prevailing conditions. As such, the prevalence of meningeal worm in a deer population also represents the best measure of the risk of

sympatric moose developing neurologic disease. The reported prevalence of *P. tenuis* in deer varies from <1% to >90% (see list of reports in Anderson and Prestwood 1981) but surprisingly little is known about the dynamics and relative importance of the many epizootiological parameters that act to establish and cause change in the prevalence of infection in the population. Prevalence typically is determined by looking for adult *P. tenuis* in the heads of deer killed during the fall hunting season. Alternatively, feces are examined for dorsal-spined larvae. Such samples are often collected in winter off snow to avoid contamination with free-living soil nematodes. In addition to possible differences related to season, there is ample evidence that prevalence data based on the presence of worms in heads can be substantially different from that based on the number of animals passing larvae (Anderson and Prestwood 1981, Thomas and Dodds 1988, Garner and Porter 1991, unpubl. data).

Intuitively, the prevalence of a parasite is influenced by host population density. Yet, in the few studies in which deer densities were actually noted, no consistent correlation with the prevalence of *P. tenuis* is apparent. Karns (1967) in Minnesota and Behrend and Witter (1968) in Maine found the parasite most prevalent in areas where deer densities were highest while Gilbert (1973), also working in Maine, found the reverse. Thomas and Dodds (1988) and Garner and Porter (1991) found no correlation between prevalence and deer density. In our study, the overall prevalence increased from a low of 32% in 1986-87 to 45%,44%, and 52% in 1987-90, respectively, during a period in which deer densities increased only moderately. Using a model based on Lenarz (1991), pre-fawning estimates of deer density in the summering area of deer sampled were 1.4, 1.6, 1.5, 2.0, 2.3, 1.8, 2.4, and 2.8/km^2 from 1984-91, respectively (pers. comm. Mark Lenarz, MN Department of Natural Resources, Grand Rapids, MN).

Clearly, there are factors more important than deer density that determine the prevalence of *P. tenuis*. Anderson and Prestwood (1981) suggested several, including climatological factors that influence the survivorship of first-stage larvae and the abundance, distribution and movement of suitable gastropod intermediate hosts. Deer habitat preferences, as well as the immunological history of the herd were also thought likely to be important.

Three previous studies document that the prevalence of *P. tenuis* can change significantly over the period of a few years. In Maine the prevalence declined from 80% in 1968 to 63% two years later (Gilbert 1973). It was thought that reduced rainfall during the period may have decreased the availability of gastropods resulting in lowered prevalence. In Nova Scotia, Brown (1983) found that the prevalence of larvae in feces changed from 14% to 71% over a 3-year study; the year of low prevalence was particularly dry. In the Upper Peninsula of Michigan, Schmitt *et al.* (1989) found 76% of deer infected in 1982 and 65-59% in 1987-89. Possible causes of these changes were not identified.

The low prevalence seen in deer of the Grand Marais area in 1986-87 can best be explained by low rainfall received 2 years before the study began. Fawns sampled in 1986-87 were infected at about the same rate as fawns in all subsequent years of the study. But the prevalence in yearlings sampled in 1986-87 (32%) was lower than that seen in yearlings examined in 1987-90 (58-65%)($P<0.01$). Most yearlings examined in 1986-87 would have acquired their infection as fawns over the summer and fall of 1985. Because of the time estimated for larvae to reach the infective stage in gastropods at field temperatures, it might be concluded that many of the snails and slugs involved in transmission to the 1985 fawn crop were in fact infected during the snow-free period of the

previous year. Interestingly, May-August of 1984 was one of the driest in the past 12 years (24.3 cm total precipitation compared to 32.3 cm 12-yr average); 1983 was another dry summer with only 26.2 cm. Also, the mean summer temperature in 1984 was about average but the snow-free period was the longest in the past 12 years (245 days). Therefore, despite an unusually long period in 1984 in which infection of gastropods could have occurred, the low precipitation received from May to August may have been the principal factor responsible for the lower prevalence in deer born in 1985 (and sampled as yearlings in 1986-87). The abundance and movement of gastropods were probably reduced during the drier summers of 1983 and 1984 but lower survival of first- stage larvae in feces and soil during these periods may also have occurred and reduced the rate of *P. tenuis* transmission.

May-August rainfall for each of the 5 summers following 1984 was above average and may explain the increase in overall prevalence seen in each of the years from 1987- 90. A return to drier summers in 1990 and 1991 may result in a lower rate of transmission to fawns born in 1991 and 1992 and be detected in future samples.

In our study, the prevalence of *P. tenuis* varied with season; more deer passed larvae in spring and summer. Thomas and Dodds (1988) found the fewest deer passing larvae in summer. Foreyt and Trainer (1980), who also measured prevalence by the frequency of larvae in feces, found it to be highest in deer at one Wisconsin site in April-June but highest at another in October; it declined at both sites over winter. Deer densities and habitat varied at the two sites but observed differences in peak prevalence were not explained.

Prevalence varied with the age of deer. It rose quickly in fawns in the Grand Marais population and by the time they were 15 mths old had reached levels of infection similar to those seen in deer of older age classes. Several authors report a similar rapid increase in prevalence with increasing age (Anderson 1963, Behrend and Witter 1968, Behrend 1970, Beaudoin *et al.*. 1970, Thurston and Strout 1978, Dew 1988, Garner and Porter 1991).

It is difficult to explain why the prevalence of infection (as measured by larvae in feces) reaches a maximum in yearling deer but apparently goes no higher in older age classes. Possibly, older deer are less susceptible and if they escape infection in the first 15 months of life, they may remain free of infection as adults. Alternatively, some deer may become infected early in life but cease passing larvae in two or three years. A premunition immunity might prevent reinfection. Little or no change would be detectable in the overall prevalence if, at the same time, animals not infected as fawns and juveniles later became infected and passed larvae. Since adult *P. tenuis* are likely long lived, this latter explanation would be supported by finding that most older deer have adult worms in the cranium and many of them are not passing larvae. Examination of both the head and feces of the same deer is required to determine if this occurs. To our knowledge, only two studies exist where this has been done. Garner and Porter (1991) did demonstrate that some deer will be infected but not pass larvae. In a subsample of 26 deer with adult worms, only 20 of them were passing larvae in their droppings. Specific ages were not given. As well, 8 deer had larvae in feces yet no adults could be found in the cranium. Earlier, Anderson (1963) concluded that a higher measure of prevalence might be expected from examining feces because worms can be in obscure locations, including the vertebral column, where they might not be found. Of 17 deer with larvae in their droppings, *P. tenuis* could only be found in the cranium of 12 (Anderson 1963).

Although small sample sizes are a universal problem in examining older age classes, the study of Karns (1967) provides the strong-

est evidence that most deer in a population eventually become infected. All of 19 animals older than 4.5 yr (in a sample of 140 heads) had worms; the overall prevalence in that population was 49% (Karns 1967). Behrend and Witter (1968) reported similar results. Other studies indicate, however, that many older animals can be free of adult worms (Anderson 1963, Beaudoin *et al.* 1970). A long term experimental study determing the life span of *P. tenuis* and the course of larval output by deer following single and repeated infections would greatly assist interpretation of these field data. Larger, carefully examined samples of both heads and feces of wild deer would also help to determine if infection of older deer can occur and to what extent they contribute to total larval production by the parasite. In clarifying this question, the possibility should also be excluded that deer under study may be infected concurrently with other elaphostrongyline nematodes that produce similar dorsal-spined larvae.

There is no clear relationship between the prevalence of infection and sex of deer. Anderson and Prestwood (1981) reviewed all reports up to that time. Many appeared to indicate that females tended to be more frequently infected than males (as reported here), while others detected no difference. Sex related behavioral differences may predispose one sex to greater contact with infected gastropods as suggested by Gilbert (1973) but better data free of sampling distortion, particularly with respect to age, seem to be required to confirm a real difference.

Fawns and yearlings passed more larvae than older animals. This probably reflects the higher larval output expected following recent infection of naive animals (Anderson 1963). Clearly, fawns passing larvae before they were 1 yr old were infected in the summer or fall of their first year. One fawn must have been infected before the middle of July when it was less than 6 weeks old. Apparently, infection of fawns continued throughout the fall and possibly until mid-Novemeber when snow fall begins and deer move to the wintering area near the shore of Lake Superior. Snow cover usually lasts in this area until mid-April and deer disperse. But patches of vegetation may be exposed as early as mid-March, allowing a brief opportunity for infection to occur while deer are still aggregated. Higher rates of infection in gastropods might be expected in the wintering area and the deer remaining over summer may experience greater risk of infection. Some of the yearlings passing relatively high numbers of larvae into the summer may not have become infected until the spring period.

Samuel *et al.* (1985) concluded that most transmission of *P. odocoilei* to mule deer in Jasper National Park occurred after animals arrived on their winter range in the river valley, beginning in August. Fawns first picked up infected gastropods in early September and by January, 100% of them were passing larvae in their droppings. The prepatent period for *P. odocoilei* is about 53 days compared to 90 days for *P. tenuis*. Peak output of first-stage larvae by infected animals also occurred while mule deer were still on winter range (March-April).

In the Grand Marais samples, *P. tenuis* larvae were passed in greatest numbers by white-tailed deer of all ages in the spring (March-May). A number of closely related elaphostrongyline nematodes follow the same pattern (Samuel *et al.* 1985, Halvorsen *et al.* 1985, Lankester and Hauta 1989). As discussed above, a spring rise in larval numbers in fawns and yearlings is expected following recent infection. However, since there is no evidence of appreciable rates of reinfection of older animals, the increased number of larvae produced by them in spring may result from increased productivity of established female worms or increased success of developing eggs and larvae in the lungs. Halvorsen *et al.* (1985) also saw a yearly cycle of larval output by older reindeer (*Rangifer tarandus tarandus*)

infected with *Elaphostrongylus rangiferi*. The greatest number of larvae were passed by males in autumn/early winter and by females in late winter/spring. Increases coincided with the rut and parturition and were thought to result from a suppressed immune response at those times.

We conclude that prevalence data are a convenient, composite measure of the many factors which interact to influence the overall success of *P. tenuis* and its transmission within a deer population. However, sampling must be standardized as much as possible for comparisons between areas to be meaningful. To a greater extent, prevalence reflects the suitability of climate and habitat for gastropods and possibly, patterns of deer behaviour that affect transmission. But the time of year at which sampling is done, the proportion of younger deer sampled, and whether heads or feces are examined can significantly affect the data.

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