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INFRAPOPULATION DYNAMICS OF *PARELAPHOSTRONGYLUS TENUIS* IN WHITE-TAILED DEER

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ABSTRACT: The prevalence and intensity of *Parelaphostrongylus tenuis* was determined by examining the head and a fecal sample from each of 379 white-tailed deer (*Odocoileus virginianus*) of known age that had been killed by vehicles in northeastern Minnesota (USA), November 1991 to May 1993. Small numbers of adult worms (mean ± SD, 3.2 ± 2.2; maximum, 13) were found in the cranium of 311 (82%); but over a third (118 of 311) of the infected deer were not passing larvae in their feces. Most occult infections were sterile because only one sex of the parasite was present. Adult *P. tenuis* were not found in the vertebral canal of deer. Prevalence of adult worms and larvae was lower in fawns (68% and 35%, respectively) than in older age classes of deer (89% and 63%, respectively). Forty-three of 45 deer between 7 and 15 yr old were infected. Mean (±SD) intensity of adult worms was lower in fawns (2.7 ± 1.8) and yearlings (3.0 ± 2.1) than in deer 7 to 15 yr (4.1 ± 2.5). Conversely, the mean (±SD) number of larvae in feces was higher in fawns (103 ± 119 larvae/g) than in adults 2 to 6 yr old (36.2 ± 46 larvae/g) and 7 to 15 yr old (35.6 ± 60 larvae/g). Mean (±SD) fecundity of female worms was greatest in fawns (51.6 ± 64.8 larvae/g of feces/female worm). Deer of all ages passed more larvae in the spring. Deer from an area where year-round density was 30 deer/km² had a mean (±SD) of 3.5 (±1.8) adult worms; deer from the study area, with a summer density 2 deer/km², had 3.2 (±2.2) worms; however, deer at the greater density passed a greater mean number of larvae (93.8 and 57.1 larvae/g, respectively). Based on our results we propose that *P. tenuis* is a long-lived parasite and that most deer become infected in their first or second summer of life, and acquire few additional worms thereafter.

Key words: *Parelaphostrongylus tenuis*, *Odocoileus virginianus*, white-tailed deer, infrapopulation.

INTRODUCTION

The meningeal worm, *Parelaphostrongylus tenuis*, is a common and widely distributed parasite of white-tailed deer (*Odocoileus virginianus*) in eastern North America (Anderson and Prestwood, 1981). Infections in this normal definitive host are relatively benign but severe neurologic disorders can result in a variety of other ungulates (Anderson and Prestwood, 1981). In areas where infected white-tailed deer are sympatric with moose (*Alces alces*) or other cervids, *P. tenuis* is an important management consideration (Whitlaw and Lankester, 1994a). However, much remains to be learned about its biology and transmission within white-tailed deer populations before its importance as a pathogen to other wild species can be completely assessed.

Prevalence and mean intensity of *P. tenuis* infection likely both are important variables in determining the rate of transmission of this parasite; it currently is unclear as to which best reflects the rate of transmission among deer and the risk of infection to other cervids. Saunders (1973) reported that where the prevalence of *P. tenuis* was high in white-tailed deer, moose densities were low. On the other hand, Whitlaw and Lankester (1994b), in a wider study of co-habiting deer and moose in Ontario, found moose density to be independent of the prevalence of the parasite in deer but inversely related to the intensity of larvae in deer feces. Other authors have failed to find any consistent relationship between the prevalence of *P. tenuis* and the density of white-tailed deer (Peterson and Lankester, 1991).

In the present study, a relatively large number of vehicle-killed deer of known age were available throughout much of the year from a population of known density. Adult *P. tenuis* in the head, and larvae in feces of the same animal, were counted.

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Our objective was to test for relationships between deer age class, sex, density, season of the year, and the prevalence and intensity of *P. tenuis*, that might influence transmission rates of the parasite in nature.

MATERIALS AND METHODS

The head and approximately 20 g of feces were collected from each of 379 deer from 10 November 1991 to 31 May 1993 in a traditional, white-tailed deer, wintering area along the northwestern shore of Lake Superior, in the vicinity of Grand Marais, Minnesota (USA) (47°45′N, 90°30′W). In summer, deer ranged ≤20 km inland and their pre-fawning density in spring of the year was estimated to be 2 deer/km² (Lenarz, 1993). Most (n = 370) animals examined were killed by vehicles between October and April; in addition three were killed by predators, two by hunters, and four died from miscellaneous causes. Specimens were stored at −20 C until examined. Sex and date of death were recorded for each individual. Age was determined by tooth eruption for fawns and yearlings (Severinghaus, 1949) and cementum ring counts for adults (Gilbert, 1966).

To evaluate the relation between deer density and prevalence and mean intensity of infection, a sample of heads and feces from a high density deer area also was examined. Thirty-four animals were shot in March 1993, in The Twin Cities Army Ammunition Plant (Arsenal), a fenced enclosure located approximately 10 km north of St. Paul, Minnesota (USA) (45°00′N, 93°06′W). The year-round density of animals in this area was estimated to be 30 deer/km² (P. Jordan, pers. comm.).

At necropsy, heads were cut sagitally, while still frozen, using a butcher's bandsaw and thereafter allowed to thaw for at least 24 hr. Shearing the hair on the dorsal surface of the head using animal clippers prevented the saw blade from jamming. Only heads free from gunshot wounds and skull fractures due to vehicle collision were examined for adult *P. tenuis*. The two halves of the brain were removed from the cranium allowing their surfaces and the exposed inner surface of the dura to be examined for worms using a hand lense and stereoscopic microscope at 1.5 to 12.5×. Subsequently, the dura was stripped from the brain case and all venous blood sinuses, including the cavernous, intercavernous, transverse and sagittal sinuses were cut open in saline and examined at 6.4 to 40×. Toothed forceps inserted into foramena along cranial nerves were gently extracted to remove any worms that might be present.

The oral cavity and pharynx of 62 heads were examined to determine if larvae could be detected here when they also were present in feces. The back of the oral cavity in each half of the cut head was doused with water. Rinsings were drained into a glass funnel. The funnel, with a short length of neoprene hose and clamp at the bottom, was covered with 2 mm mesh screening to catch any hair and undigested food particles. After settling for at least 1 hr, the sediment was drained from the funnel into a watch glass with a grid etched on the bottom, and examined for larvae.

Data recorded for each head included number and sex of nematodes as estimated from the number of intact worms plus the number of additional matched anterior and posterior ends of broken worms; presence of grossly visible lesions; and location of worms. The sex of broken worms was determined by the presence of eggs or sperm (100×). A sample of intact worms was measured in saline with the aid of a drawing tube at 100× and preserved in 10% glycerin in 70% ethanol.

To determine if any adult *P. tenuis* resided in the vertebral canal, the head and spine were examined from 26 deer. The frozen vertebral column was initially cut into four equal segments, each of which was cut sagitally with a bandsaw and allowed to thaw for 24 hr. The spinal cord was removed by severing the spinal nerves and the leptomeningeal surfaces and the spinal dura mater were examined using a stereoscope at 1.5 to 12.5×. Following visual examination of membranes and surface of the spinal cord, all tissues were agitated vigorously in water in a settling flask. The flask was later decanted and the sediment examined for worms. The epidural space was examined by scraping away fat deposits with forceps. Toothed forceps were inserted into foramena and gently pulled out along spinal nerves to extract any hidden worms.

Weighed samples of feces from each deer were examined for dorsal-spined, first-stage larvae using the Baermann technique as described by Peterson and Lankester (1991). Larvae were counted and expressed as numbers per gram of fresh feces. A sample of feces (n = 100) was randomly collected off snow in March 1993 to compare prevalence of infection with that in the road killed sample taken in March 1993 (n = 50).

All deer were considered to have been born 1 June. Data were analyzed using four grouped age classes: fawns (<1 yr), yearlings (1-yr-olds), 2- to 6-yr-olds, and 7- to 15-yr-olds. Analyses of seasonal differences were done by pooling data according to fall (September through November), winter (December through February), and spring (March through May). Sample sizes be-

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tween June and August were low ($n = 4$), therefore deer collected in this period were omitted from seasonal analyses.

Data were evaluated using the Statistical Package for the Social Sciences (SPSS). Tests for significance ($P < 0.05$) were done using univariate and heterogeneity chi-square (χ^2), Mann-Whitney U, Kruskal-Wallis and multiple comparisons, and Spearman's rank correlation (r_s) (SAS Institute Inc., 1985; Zar, 1984) to determine if variables were independent.

RESULTS

Adult *P. tenuis* were present in the cranium of 311 (82%) of 379 deer killed by vehicles; only 202 (53%) animals were passing dorsal-spined larvae in their feces (Table 1). The prevalence of larvae in the feces of vehicle-killed animals did not differ from that in feces collected from the deer wintering range.

Most ($n = 150$) infected deer passing larvae had both sexes of worm present in the cranium, but 43 had only one sex of worm present (29 with only females, 14 with only males); no worms were detected in nine deer shedding larvae. Ninety-two of the 118 infected deer not passing larvae had only one sex of *P. tenuis* present and 26 had both sexes. Eighteen (69%) of the 26 infected with both worm sexes were <2 yr and may not have been infected long enough for worms to mate and for larvae to appear in the feces.

Prevalence of adult worms in the cranium varied with age of deer, regardless of sex or year of collection. Based on the heterogeneity chi-square test, there were no differences in prevalence between collection years or between sexes; thus, year and sex data were pooled for further analyses. Prevalence of adult worms in the cranium was lower ($\chi^2 = 26.5$, $P < 0.001$) in fawns (68%) than in the three older age classes (89%); the three older age classes did not differ significantly from each other (Table 1). Forty-three of 45 deer >6 yr had worms in the cranium. Prevalence of worms varied with season in the fawn age class ($\chi^2 = 9.2$, $P < 0.009$), but not in animals older than one year. Within fawns, prevalence of worms was lower in fall (43%) than in winter (68%) ($\chi^2 = 3.84$, $P = 0.049$) and in spring (79%) ($\chi^2 = 9.29$, $P = 0.002$) (Table 2).

TABLE 1. Prevalence (%) of *Parelaphostrongylus tenuis* by age of white-tailed deer collected in northeastern Minnesota, November 1991 to May 1993.

Age (yr)	Number of deer examined	Prevalence (%)		
		Adults in heads	Larvae in feces	Overall prevalence[a]
<1	132	68 (90)[b]	35 (46)	71 (93)
1	85	87 (74)	58 (49)	91 (77)
2 to 6	117	89 (104)	66 (77)	92 (107)
7 to 15	45	96 (43)	67 (30)	96 (43)
Total	379	82 (311)	53 (202)	84 (320)

[a] Percent of deer infected with larvae in the feces, adult worms in the cranium, or both.
[b] Prevalence (number of deer infected).

Prevalence of larvae in the feces similarly varied with age of deer, regardless of the sex or year of collection. Based on the heterogeneity chi-square test, there was no difference in prevalence between collection years or between sexes. Prevalence of larvae was lower in fawns (35%) than in the three older age classes (63%) ($\chi^2 = 27.7$, $P < 0.001$); the three older age classes did not differ from each other (Table 1). Prevalence of larvae in feces also varied with season in the fawn age class ($\chi^2 = 21.48$, $P < 0.001$) but not in animals older than one year. Within fawns, prevalence of larvae was lower in fall (5%) than in winter (25%) ($\chi^2 = 4.2$, $P = 0.03$) and in spring (58%) ($\chi^2 = 16.6$, $P < 0.001$) (Table 2).

Intensity of adult worms in the cranium and larvae in the feces of infected animals did not differ between years or sex of deer and data were pooled for further analyses. Overall, infected deer had a mean ± SD of 3.2 ± 2.2 adult *P. tenuis* with a maximum of 13 in one deer. The mean intensity of adult worms in the cranium increased with the age of deer ($r_s = 0.20$, $P < 0.001$). It was lower in fawns (2.7 ± 1.8) and yearlings (3.0 ± 2.1) than in adults 7 to 15 yr old (4.1 ± 2.5); adults 2 to 6 yr old (3.5 ± 2.5) did not differ from other age classes ($H = 14.6$, $P = 0.002$). Conversely, the mean intensity of larvae in feces decreased

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TABLE 2. Seasonal prevalence and mean intensity of *Parelaphostrongylus tenuis* in heads and feces of white-tailed deer collected in northeastern Minnesota, November 1991 to May 1993.

Age	Season	Prevalence				Intensity	
		Adults in heads		Larvae in feces		Adults in heads (mean ± SD)	Larvae per gram of feces (mean ± SD)
<1	Summer	NA[a]	(0/0)[b]	NA	(0/0)	NA	NA
	Fall	43[c]	(9/21)	5	(1/21)	1.8 ± 0.9	0.2 ± NA
	Winter	68	(40/59)	25	(15/59)	2.7 ± 2.0	52.3 ± 58.1
	Spring	79	(41/52)	58	(30/52)	2.8 ± 1.8	131.8 ± 133.3
	Total	68	(90/132)	35	(46/132)	2.7 ± 1.8	102.9 ± 118.9
>1	Summer	75	(3/4)	50	(2/4)	1.7 ± 0.6	39.8 ± 53.8
	Fall	93	(28/30)	56	(17/30)	3.5 ± 2.5	11.2 ± 13.2
	Winter	88	(77/88)	60	(53/88)	3.8 ± 2.5	33.1 ± 41.2
	Spring	90	(113/125)	67	(84/125)	3.2 ± 2.2	57.0 ± 64.4
	Total	89	(221/247)	63	(156/247)	3.4 ± 2.4	43.5 ± 55.3
Overall	Summer	75	(3/4)	50	(2/4)	1.6 ± 0.6	39.8 ± 53.8
	Fall	73	(37/51)	35	(18/51)	3.1 ± 2.3	10.6 ± 13.0
	Winter	80	(117/147)	46	(68/147)	3.4 ± 2.4	37.5 ± 45.7
	Spring	87	(154/177)	64	(114/177)	3.1 ± 2.1	76.8 ± 93.5
	Total	82	(311/379)	53	(202/379)	3.2 ± 2.2	57.1 ± 78.4

[a] NA, not applicable.
[b] Number of animals infected/number of animals examined.
[c] Percent positive.

with the age of deer ($r_s = -0.28$, $P < 0.001$). The mean (±SD) number of larvae per gram of feces was greater in fawns (102.9 ± 118.9 larvae/g) than in adults 2 to 6 yr old (36.2 ± 45.9 larvae/g) and 7 to 15 yr old (35.6 ± 60.0 larvae/g) ($H = 13.17$, $P = 0.004$); yearlings (59.8 ± 64.7 larvae/g) did not differ from the two adult age classes. The mean ± SD length of adult worms (females, 89 ± 8 mm, range 60 to 104 mm; males, 63 ± 8 mm, range 50 to 89) was not correlated with the age of deer from which they were recovered.

Deer of all ages passed more larvae in spring (mean ±SD, 76.8 ± 93.5 larvae/g of feces) than in fall (10.6 ± 13.0 larvae/g) and winter (37.5 ± 45.7 larvae/g) ($H = 17.6$, $P = 0.0002$). Yet, the mean number of adult worms in heads did not vary with season ($H = 3.2$, $P = 0.20$) (Table 2).

When only those animals passing larvae and with adult female worms in their heads were considered, the intensity of larvae in feces was not correlated with the number of adult female *P. tenuis* in the cranium ($r_s = 0.11$, $P = 0.06$). However, intensity of larvae in feces was correlated with location of female worms ($r_s = 0.58$, $P < 0.001$); as the ratio of female worms in the venous sinuses to subdural space increased, so did the number of larvae released in the feces.

Mean fecundity of female worms was defined as the mean number of larvae/gram of feces/female worm only in deer with both female *P. tenuis* in their heads and larvae in their feces; mean fecundity of female worms decreased with the age of deer ($r_s = -0.34$, $P < 0.001$) (Table 3). Mean (±SD) fecundity was greater in fawns (51.6 ± 64.8 larvae/gram of feces/female worm) than in adults 2 to 6 yr old (14.6 ± 26.3 larvae/g/female worms) and 7 to 15 yr old (11.6 ± 27.9 larvae/g/female worms) ($H = 19.13$, $P = 0.0003$); yearlings (28 ± 30.7 larvae/g/female worms) did not differ from fawns or the two adult age classes. Mean fecundity was greater in spring (44.1 ± 52.3 larvae/g/female worms) than in fall (6.3 ± 9.1 larvae/g/female worms) ($H = 18.37$, $P = 0.0001$).

Although the highest proportion of uni-

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TABLE 3. Fecundity of female *Parelaphostrongylus tenuis* by age of white-tailed deer collected in northeastern Minnesota, November 1991 to May 1993.

Age of deer (yr)	Mean number of female worms per infected deer ± SD	Mean number of larvae per g ± SD	Mean fecundity[a] ± SD
<1	2.0 ± 1.2 (79/39)[b]	103.2 ± 105.2	51.6 ± 64.8
1	2.3 ± 1.4 (99/44)	64.4 ± 66.6	28.0 ± 30.7
2 to 6	2.5 ± 1.8 (171/69)	36.5 ± 46.3	14.6 ± 26.3
7 to 15	3.3 ± 2.0 (89/27)	38.3 ± 59.4	11.6 ± 27.9
Total	2.4 ± 1.7 (438/179)	58.1 ± 74.1	24.2 ± 40.8

[a] Mean number of larvae per gram of feces/female worm.
[b] Mean ± SD (total number of female worms/number of deer with female worms in their head and larvae in their feces).

sexual infections (40%) was found in the fawn age class, it did not change significantly in older age classes of deer (Table 4). Bisexual, occult infections were most frequent in fawns (12%). The overall sex ratio of adult worms was 1.5 females:1 male and did not change with age of deer (Table 5).

The four venous blood sinuses (sagittal, transverse, cavernous and intracavernous), collectively, were occupied more frequently (58%, $n = 578$) than the subdural space (40%, $n = 403$) (Table 6). The ratio of worms in the sinus to subdural space did not change with age of deer.

Worms located on the dura of most deer were partially embedded under delicate fibrinous strands associated with little, if any, inflammatory exudate. In 22 deer, the dura was thickened and covered by a yellowish-red exudate in the vicinity of the worms. All but five of these latter animals were >2 yr old. In 29 deer, of which 25 were older than 2 yr, the sagittal and transverse blood sinuses were occluded with masses of up to 10 worms. Thickening of the sinus walls and inflammatory exudate invariably were associated with such masses. When the exudate was pressed between glass plates and examined under the stereo-microscope (40×), numerous eggs and active larvae were seen. Only three adult deer had worms located within the pia-arachnoid with portions of the worms penetrating between sulci of the brain, but none appeared to penetrate the neural tissue. No evidence of dead or moribund worms was observed.

Only one of 26 vertebral canals from deer >1 yr contained *P. tenuis*. This was a subadult female worm found in a 3-yr-old female deer killed on 15 January that was passing larvae in its feces and had adult worms of both sexes in its cranium. The worm was flushed from the vertebral

TABLE 4. Proportion of unisexual and bisexual *Parelaphostrongylus tenuis*, occult infections by age class of white-tailed deer collected in northeastern Minnesota, November 1991 to May 1993.

Age (yr)	Number of deer with worms in the cranium	Percent occult infections	
		Unisexual (*n*)	Bisexual (*n*)
<1	90	40% (36)	12% (11)
1	74	28% (21)	8% (7)
2 to 6	104	24% (25)	6% (5)
7 to 15	43	23% (10)	3% (3)
Total	311	30% (92)	8% (26)

TABLE 5. Sex ratio of *Parelaphostrongylus tenuis* by age class of white-tailed deer collected in northeastern Minnesota, November 1991 to May 1993.

Age (yr)	Total number of female worms	Total number of male worms	Ratio of f:m
<1	133	101	1.3:1
1	134	88	1.5:1
2 to 6	214	145	1.5:1
7 to 15	113	63	1.8:1
Total	594	397	1.5:1

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TABLE 6. Numbers of *Parelaphostrongylus tenuis* found in venous blood sinuses and the subdural space by age class of white-tailed deer collected in northeastern Minnesota, November 1991 to May 1993.

Age (yr)	Number of deer infected	Total worms	Number of worms in the sinuses	Number of worms in the subdural space	Ratio*
<1	90	234	125	108	1.2:1
1	74	221	138	80	1.7:1
2 to 6	104	359	220	136	1.6:1
7 to 15	43	177	95	79	1.2:1
Total	311	991	578	403	1.4:1

* Ratio of worms in sinuses to subdural space.

canal and the precise location was not determined.

Larvae were detected in the oral cavity of 44 deer, all of which had larvae in their feces; larvae were not found in oral cavity washes of 18 animals whose feces were negative. Apparently, in the absence of fecal samples, washes of the oral cavity can be relied upon to detect deer passing larvae.

Thirty-four additional deer heads and fecal samples were examined from a location where deer density was known to be unusually high (Arsenal). The prevalence of adult worms did not differ significantly between deer at the Arsenal (94%) and at Grand Marais (82%). However, prevalence of larvae was higher in the Arsenal animals (77%) than in those from Grand Marais (53%) ($\chi^2 = 6.7$, $P = 0.01$) (Table 7). The mean (±SD) intensity of adult worms in the Grand Marias animals (3.2 ± 2.2) did not differ significantly from that in the Arsenal animals (3.5 ± 1.8), but the Arsenal animals passed a greater mean number of larvae (93.8 ± 82.3 larvae/g) than those from Grand Marais (57.1 ± 78.4 larvae/g) ($U = 1{,}802.5$ $P = 0.01$). Moreover, the mean fecundity of female worms was higher in the Arsenal animals (42.6 ± 50.2 larvae/g/female worms) than in those from Grand Marais (24.2 ± 31.2 larvae/g/female worms) ($U = 2326.0$, $P = 0.002$).

DISCUSSION

In our study, about 80% of white-tailed deer became infected with *P. tenuis* during their first summer and fall of life. This fawn cohort provides the only available measure of annual incidence of infection. It is important, however, that the fawns be sampled late enough in winter to allow sufficient time for migrating worms to be detectable in the cranium. The rapid infection of young animals was similarly observed by Peterson and Lankester (1991) in an earlier study of deer feces in the Grand Marais area, and by Bogaczyk et al. (1993) in Maine. Samuel et al. (1985), studying a closely related nematode, *P. odocoilei*, in mule deer (*Odocoileus h. hemionus*), found that fawns first picked

TABLE 7. Prevalence and mean intensity of *Parelaphostrongylus tenuis* in heads and feces of white-tailed deer collected from two localities of differing deer densities: Grand Marais (November 1991 to May 1993) and the Arsenal (March 1993).

				Adults in heads		Larvae in feces		
Location	Deer/km²	Age (yr)	Number of deer examined	Prevalence (%)	Mean intensity ± SD	Prevalence (%)	Mean intensity ± SD (N)	Overall prevalence*
Grand Marais	2	<1	132	68	2.7 ± 1.8	35	102.9 ± 118.6 (46)	71
		>1	247	90	3.4 ± 2.4	63	43.5 ± 55.3 (156)	92
Total			379	82	3.2 ± 2.2	53	57.1 ± 78.4 (202)	84
Arsenal	30	<1	8	88	3.7 ± 2.6	62	134.0 ± 73.5 (5)	88
		>1	26	96	3.5 ± 1.6	81	84.1 ± 83.0 (21)	96
Total			34	94	3.5 ± 1.8	77	93.8 ± 82.3 (26)	94

* Percent of deer infected with larvae in the feces and/or adult worms in the cranium.

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up infected gastropods in September after arriving on the wintering area and by January, 100% were passing larvae in their droppings.

Mean (±SD) numbers of worms per deer (3.2 ± 2.2) did not increase with age after 1 yr, but most older white-tailed deer eventually became infected; 43 of 45 deer in the 7 to 15 yr age class were infected. Karns (1967) was the first to propose that almost all deer in an enzootic area eventually become infected with *P. tenuis*. Although his sample size was limited and feces were not examined, adult *P. tenuis* occurred in the heads of all 19 deer older than 4.5 yr. Behrend and Witter (1968) reported similar results. Others who reported a large proportion of older, uninfected deer free of infection (Anderson, 1963; Beaudoin et al., 1970), may have overlooked worms in the cranium.

Over one-third of the deer with adult *P. tenuis* in the cranium passed no larvae in their feces. Some of these occult infections in fawns and yearlings probably were prepatent, but most in older animals were sterile because only one sex of the parasite was present. Low availability of infective larvae in gastropods (Lankester and Anderson, 1968), and the possibility of a rapidly established immune response, probably restrict the numbers of adult worms that can mature in individual deer; but as a consequence, the frequency of unisexual infections is high.

Some unisexual infections may have resulted from males, the smaller of the two sexes, being swept out of the cranial venous blood sinuses to other locations. The type specimen of *P. tenuis*, a male, was found in the lung of a white-tailed deer by Dougherty (1945) and originally assigned to the genus *Pneumostrongylus*. Also, males may die sooner than females, but no dead or moribund worms were observed. However, since the frequency of unisexual infections did not increase with deer age, neither of these possibilities is likely to be important.

Natural infections of *P. tenuis* established by small numbers of infective larvae apparently take longer to reach patency than has been observed in experiments with captive animals. Fawns examined herein first had adult worms in the cranium in September. Migration to this location requires about 50 days (Anderson, 1963). First-stage larvae, however, were not seen in fawn feces until mid-December and most fawns were not positive until January. This approximates a 4 to 5 mo prepatent period. Also, seven animals killed from early March to April had both sexes of worms in the cranium but were not yet passing larvae. Assuming that the opportunity to pick up infected gastropods ceased after the arrival of snow in mid-November, these animals would have been infected for at least 4 mo. Anderson (1963) found that captive fawns given 500 to 600 infective larvae first produced larvae in their feces after 80 to 91 days. Later, Anderson and Prestwood (1981) reported that patency may require 115 days or more in individual deer. Samuel et al. (1992) observed pre-patent periods from 88 to 128 days in white-tailed deer given 15 to 50 infective *P. tenuis* larvae and proposed that the time required for patency was inversely related to the infecting dose given. Patency took as long as 137 days in a white-tail given seven larvae (Rickard et al., 1994).

Prevalence of *P. tenuis* infection did not vary between the sexes or between years. Garner and Porter (1991) similarly found no difference in the prevalence between male and female deer while Gilbert (1973), who found females most frequently infected, proposed that sex-related behavioral differences in cover-type selection during fawn rearing may predispose females to greater contact with infected gastropods. However, based on our results, we believe that most female deer become infected before they ever rear young. Inconsistent differences between the sexes have been observed by several authors, as reviewed by Lankester (1987).

Age- and season-standardized samples

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are required to compare accurately the prevalence of *P. tenuis* infection among deer populations. Heads alone provide the most accurate measure of how many deer in a population are infected; the spines can be ignored. Feces, on the other hand, reveal the number of deer actually passing first-stage larvae and thereby provide estimates of total larval production by the parasite suprapopulation. Caution must be exercised, however, since other species of metastrongyloid nematodes occurring in deer pass first-stage larvae indistinguishable from those of *P. tenuis* (Lankester and Hauta, 1989). The deer population that winters at Grand Marais appears to be free of *P. andersoni* (Peterson and Lankester, 1991).

Based on our results, we propose that *P. tenuis* is long-lived in white-tailed deer. The limited number of adult worms, their sex ratio, and the proportion of unisexual infections, all remained unchanged in deer ranging from 2 to 15 yr old. Although worms in older deer often were surrounded by exudate and adherent to the meninges, no dead or moribund worms were found. Other species in the family Protostrongylidae also may live for several years. Watson (1984) reported that *Elaphostrongylus cervi* lives for up to 6 yr in red deer (*Cervus elaphus elaphus*) and an experimentally infected mule deer passed larvae of *P. odocoilei* for 9.4 years (W. M. Samuel, pers. comm.).

If *P. tenuis* in white-tailed deer is equally long-lived, the first few infective larvae ingested over an animal's first or second summer must initiate a protective immunity that restricts further infection and establishes a limited, threshold number of adult worms. The age of worms found then would approximate the age of the deer. Prestwood and Nettles (1977) demonstrated that white-tailed deer develop an immunity to *P. andersoni* and resist subsequent challenge infections. Deer also produce a strong eosinophilic response upon infection with *P. tenuis* (Anderson and Strelive, 1967). On the other hand, the lack of correlation between worm length and deer age and, the recovery of one immature *P. tenuis* in the vertebral canal of an already infected, 3-yr-old deer, seems inconsistent with the hypothesis that worms are long-lived and deer are immune to reinfection. However, *P. tenuis* may not continue to lengthen with age and the immature worm may have been incapable of reaching the cranium. Alternatively, the immune protection of infected deer may not be absolute and recruitment of new worms may continue at a low rate or vary with an animal's immunological responsiveness.

The number of infective larvae of *P. tenuis* required to be ingested to establish the relatively low number of persistent worms present in wild white-tailed deer is unknown. In heavily infected experimental deer, only four to 25 worms reached maturity for every 500 to 600 infective larvae given (Anderson, 1965). But the success of migrating larvae may be greater when the number of invading larvae is low. Rickard et al. (1994) recovered three *P. tenuis* from a white-tailed deer given six infective larvae. On average, naturally infected gastropods harbor fewer than three infective *P. tenuis* larvae (Lankester and Anderson, 1968). Apparently few would have to be ingested by a deer to establish a typical *P. tenuis* infection. In the northern part of their range, white-tailed deer fawns have only 5 to 6 mo to acquire infection before snow falls. During winter, sufficient immune response may develop to prevent appreciable, future infection. A longer, uninterrupted transmission period may explain why white-tailed deer in some southern areas reportedly have slightly greater numbers of worms (Anderson and Prestwood, 1981). The few massive infections of *P. tenuis* reported in wild deer (Prestwood and Smith, 1969; Prestwood, 1970) may result from lowered resistance (Anderson and Prestwood, 1981) or from ingesting heavily infected gastropods over a short period of time. Heavily infected gastropods occur but are rare. Of

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almost 10,000 terrestrial gastropods examined by Lankester and Anderson (1968) from Navy Island, Ontario, only three of 426 infected ones had more than 5 larvae; one *Deroceras laeve* had 97 larvae.

The greatest numbers of *P. tenuis* larvae are released by young, recently infected deer. Anderson (1963) proposed that the higher larval output in fawns was due to recent infection of naive animals. Declining larval production by older deer could result from decreased egg output by older female worms or by increased host immune response to eggs and larvae developing in the lungs. Individual effects of these two components could not be separated in our measurement of female fecundity. Fecundity was calculated here by apportioning larvae counted in feces with the number of female worms in the head. Female worms in young deer were the most fecund.

Larval output increased in deer of all ages in the spring. Increased reproductive activity of female worms may be triggered by seasonal changes; also, deer experiencing nutritional stress in spring may be immunologically compromised, allowing more larvae to develop and pass from the lungs. Other closely related elaphostrongyline nematodes also have a spring rise in larval output, including *P. odocoilei* in mule deer (Samuel et al., 1985), and *P. andersoni* in caribou (*Rangifer tarandus groenlandicum* and *R. tarandus caribou*) (Lankester and Hauta, 1989). Halvorsen et al. (1985) reported that larval production of *Elaphostrongylus rangiferi* increases in male reindeer (*Rangifer tarandus tarandus*) in the fall following the rut and in females following parturition in the spring. These changes in larval output were believed to be due to reduced host resistance.

Larval production was greatest in deer with the highest proportion of female worms located in the venous blood sinuses. Worms in the subdural space lay many of their eggs on the dura where they become enmeshed in fibrous tissue (Anderson, 1963). Larvae hatching there may have greater difficulty reaching the venous circulation. In the present study there was no evidence that worms moved from other locations into the blood sinuses with increasing age of the infection, as might occur in older age classes of deer. Similarly, Gilbert (1973) detected no difference in the location favored by worms in relation to age of deer. Thurston and Strout (1978), however, found worms most common in the tentorium cerebelli of adult deer, but in the falx cerebri of fawns. The most common site of infection in our study was the cavernous sinuses which drain directly into the jugular veins.

The number of female worms in the cranium was not correlated with the number of larvae passed in the feces. Bogaczyk (1990) reached a similar conclusion using the total number of worms, rather than just females. Possibly, the combined effects of age of infection, season, location of female worms, and the degree of host immune response, masked any correlation with numbers of female worms.

There may be a threshold number of adult *P. tenuis* accommodated by whitetailed deer that is not exceeded as deer densities and the probability of infection increase. Deer in a confined population reaching a year-round density of 30 animals/km^2 had the same number of adult *P. tenuis* as deer where the summer density was only 2/km^2. Thus, it is not surprising that Gilbert (1973) and Bogaczyk et al. (1993) found no correlation between deer density and the number of worms in the heads of infected deer.

When the threshold number of adult worms per deer is reached, infrapopulation larval production should reach a maximum, and not increase with further increases in deer density. However, the mean number of larvae passed by animals at the Arsenal was greater than that by animals in the Grand Marais population. Since the mean intensity of adult worms was the same in both populations, the greater number of larvae produced by the Arsenal deer could have resulted from a more fecund

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strain of worm or a weaker immune response by the crowded deer. Total larval production by the parasite suprapopulation would be directly related to deer density as well as to the proportion of sterile, unisexual infections. The proportion of unisexual infections might be expected to decrease, and herd larval production to increase, if gastropods were more frequently and heavily infected.

Our findings have important implications for modeling *P. tenuis* transmission within deer herds and in understanding factors that determine the risk of infection to other cervids in which the worm is pathogenic. Infrapopulation larval production may be largely independent of deer density. A low, threshold number of adult worms may determine the maximum number of larvae produced per deer. Larval production is highest in young animals and in spring of the year. However, suprapopulation larval production does increase with higher deer density. Also, the proportion of young naive deer in a population and the ability of deer to produce an effective immune response to the parasite can be expected to alter suprapopulation larval production. Favorable climatic factors may increase the mean number of infective larvae per gastropod. This is predicted to reduce the proportion of unisexual infections and possibly increase the threshold intensity in deer, and thereby increase suprapopulation larval production. Further research should be directed toward understanding ecological factors affecting the survival of first-stage larvae and the prevalence and intensity of infection in gastropods and how they may change the rate of transmission to cervid hosts.

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