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FACTORS AFFECTING *PARELAPHOSTRONGYLUS TENUIS* IN WHITE-TAILED DEER (*ODOCOILEUS VIRGINIANUS*) FROM MAINE

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ABSTRACT: White-tailed deer (*Odocoileus virginianus*) collected in Maine (USA) from November 1988 to December 1989 were examined for *Parelaphostrongylus tenuis*. Relationships of deer age class, sex, collection year, and deer density to prevalence and intensity of *P. tenuis* infections were analyzed. Prevalence increased with deer age ($P < 0.001$) and interaction of deer age class and collection year ($P < 0.001$). Prevalence did not vary by year in deer ≥1 yr old (85%, $n = 519$), but was higher in fawns in 1988 (66%, $n = 87$) than 1989 (23%, $n = 73$, $P < 0.001$). Based on such yearly variations, prevalence in fawns during late autumn could provide an index of annual transmission of *P. tenuis*. Intensity of *P. tenuis* averaged 2.5 worms per infected fawn (SD = 2.8, $n = 72$) versus 3.9 (SD = 3.1, $n = 375$) in deer ≥1 yr old ($P = 0.032$). Neither prevalence ($P > 0.50$) nor intensity ($P > 0.50$) of infection was associated with deer density over a range of 1.4 to 5.8 deer per km². Heads and fecal samples from the same individuals ($n = 42$) provided prevalence estimates of 73% and 44%, respectively. No differences in prevalence, intensity, or geographic distribution of *P. tenuis* in adult deer collected in Maine during fall were evident between the late 1980's (this study) and the late 1960's (Gilbert, 1973). Moose (*Alces alces*) populations increased from the 1960's through 1980's in areas of Maine where >80% of adult deer carried *P. tenuis*, despite the risk of a lethal neurologic disease that occurs when moose become infected with the parasite.

Key words: Maine, moose (*Alces alces*), meningeal worm, *Parelaphostrongylus tenuis*, white-tailed deer, *Odocoileus virginianus*.

INTRODUCTION

Parelaphostrongylus tenuis is common in white-tailed deer (*Odocoileus virginianus*) in eastern North America (Karns, 1967; Gilbert, 1973; Comer et al., 1991). Infection is considered benign in deer but causes fatal neurologic disorders in moose (*Alces alces*) and other ungulates (Anderson and Lankester, 1974). Hence, in areas with sympatric deer and moose herds, *P. tenuis* is of concern to wildlife managers. Recent expansion of moose herds along the southern edge of their range where white-tailed deer are present has generated controversy regarding the role of *P. tenuis* in regulating ungulate populations (Cole, 1981; Nudds, 1990).

Many studies of *P. tenuis* prevalence and intensity have been published (e.g., Behrend and Witter, 1968; Thurston and Strout, 1978; Upshall et al., 1987). However, there were few adequate tests for the effects of host age, sex, or density on infection parameters.

Specific objectives of our study were to determine relationships of deer age class, sex, density, and year of collection to prevalence and intensity of *P. tenuis* in Maine (USA) deer; compare estimates of *P. tenuis* prevalence obtained by examining deer crania for adult worms versus examining deer feces for first-stage larvae; and compare 1988 to 1989 prevalence, intensity, and distribution of *P. tenuis* in Maine with data collected in 1968 to 1970 by Gilbert (1973).

MATERIALS AND METHODS

Specimens for study were collected throughout Maine (43°00′ to 47°20′N, 67°00′ to 71°00′W) from November 1988 to December 1989. Prevalence (percentage of deer with ≥1 adult worm) and intensity (number of worms per infected

deer) of *P. tenuis* were determined by examining deer crania for adult nematodes. Deer heads were collected from meat packaging plants, winter-kills, road-kills, and poached deer by personnel of the Maine Department of Inland Fisheries and Wildlife (MDIFW) from November 1988 through December 1989. Most samples were obtained from locker plants during hunting seasons of November 1988 and 1989. Heads free of gunshot wounds or other disfigurements that would prevent cranial examination or aging were severed at the cervical vertebrae and stored frozen until examination. Fecal samples (approximately 20 g), as well as heads, were obtained whenever possible.

Examination of heads from deer killed by hunters occurred between early November and 1 January each year. Heads obtained from other sources were examined as received. After thawing, crania were opened sagitally and examined for adult worms as described by Comer et al. (1991). Adult worms are small and difficult to find; thus, some undoubtedly were missed. Deer age class (fawn = <1 yr; yearling = ≥1 and <2 yr; adult = ≥2 yr) was determined by tooth wear and replacement (Severinghaus, 1949).

Four seasons were defined: (1) fall 1988 (30 October to 26 November 1988), (2) winter 1988–89 (27 November 1988 to 15 April 1989), (3) summer 1989 (16 April to 15 September 1989), and (4) fall 1989 (28 October to 25 November 1989). Sample sizes during winter (n = 30) and summer (n = 43) periods were low; therefore, these periods were omitted from analyses of relationships of deer age class, sex, and collection year to prevalence and intensity; however, for analyses of host density, all available data were used.

Relationships among age class, sex, year, and *P. tenuis* prevalence were assessed using a general linear model analogous to a categorical analysis of variance (PROC CATMOD; SAS Institute Inc., 1985). Intensity data were ranked, and a non-parametric multiple analysis of variance was used to assess relationships among age class, sex, and year. SYSTAT (Wilkinson, 1989) was used for multiple analysis of variance and all subsequent analyses. Throughout this study, effects were considered significant if $P \leq 0.05$.

Deer density estimates for Maine's 17 Deer Management Districts (DMD's) for 1988 and 1989 were obtained from a MDIFW harvest model (Maine Department of Inland Fisheries and Wildlife, 1989) and averaged to obtain one value per DMD. Data from all seasons were used for density analyses to ensure adequate samples for all DMD's. Prevalence and intensity data from yearling and adult males and females were calculated for each DMD, and pooled because differences were not significant (prevalence: $\chi^2 = 0.14$, 1 df, $P = 0.71$; intensity: $F = 1.77$, 1 df, $P = 0.18$) (Wilkinson, 1989). Spearman's Rank Correlation was used to determine if deer density was associated with prevalence and intensity of infection (Wilkinson, 1989).

To compare methods of estimating *P. tenuis* prevalence, crania from deer were examined, and feces from the same deer were analyzed for dorsal-spined larvae using the Baermann technique (Beane and Hobbs, 1983). Glassware was sterilized by steam under pressure between samples to avoid contamination. Data from all seasons were used in these analyses to maximize sample sizes.

Parelaphostrongylus tenuis prevalence also was calculated on the basis of eight Biological Zones used by Gilbert (1973). Gilbert (1973) examined deer acquired during October and November 1968 through 1970; therefore, only our fall data were compared with his data using contingency table analyses (Wilkinson, 1989). Gilbert (1973) did not distinguish between yearlings and adults. We found no difference in prevalence ($\chi^2 = 0.14$, 1 df, $P = 0.71$) between yearlings and adults, and thus we pooled these data to compare to Gilbert's (1973) results. Fawns were excluded from this comparison because their prevalence was significantly lower than older age classes, and fawn samples sizes were small.

Our results on intensity of *P. tenuis* infections also were compared by Biological Zones as reported by Gilbert (1973). We again pooled our yearling and adult data because differences were not significant ($F = 1.77$, 1 df, $P = 0.18$). We could not statistically compare intensity data for the two time periods because Gilbert's (1973, Table 3) data lacked variance estimates.

RESULTS

We examined 679 deer heads for *P. tenuis*; 308 were from fall 1988, 30 from winter 1988–89, 43 from summer 1989, and 298 from fall 1989. Of these, 583 deer were hunter-killed, 69 vehicle-killed, 14 winter-killed, cause of death was unknown for seven, and six were confiscated from poachers.

Prevalence of *P. tenuis* in fall was associated with deer age class ($\chi^2 = 58.79$, 2 df, $P < 0.001$) and the interaction of age class and year ($\chi^2 = 14.85$, 2 df, $P < 0.001$) (Table 1). Fawns were omitted and data re-analyzed using the same procedure. Neither age class nor interaction of age and year was significant, indicating fawns

TABLE 1. Prevalence of *Parelaphostrongylus tenuis* infections in white-tailed deer collected in Maine during the fall by age and sex, 1988 and 1989.

Age[b]	Sex	Fall[a] 1988 (*n*)	Fall[a] 1989 (*n*)	Mean (*n*)
Fawn	Male	61 (44)[c]	21 (39)	NA[d]
	Female	70 (43)	26 (34)	NA[d]
Yearling	Male	86 (64)	79 (48)	83 (112)
	Female	81 (42)	93 (43)	87 (85)
Adult	Male	89 (14)	89 (9)	89 (23)
	Female	90 (99)	82 (133)	85 (232)

[a] Fall 1988 = 30 October to 26 November 1988, Fall 1989 = 28 October to 25 November 1989.

[b] Age (χ^2 = 58.79, 2 df, $P < 0.0001$) and interaction of age and period (χ^2 = 14.85, 2 df, $P = 0.0001$) was significantly associated with prevalence.

[c] Percent of deer with ≥1 adult worm (number of deer sampled).

[d] Not applicable because prevalence of 1988 fawns significantly higher (χ^2 = 28.5, 1 df, $P < 0.001$) than 1989 fawns.

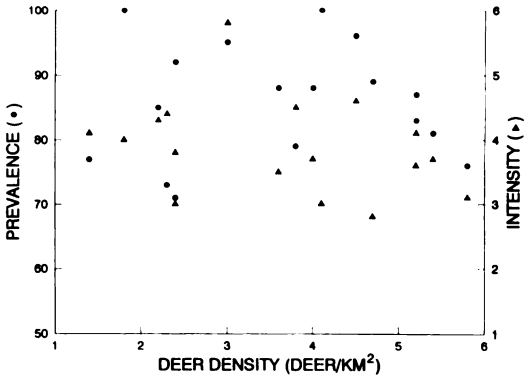

FIGURE 1. Prevalence (percentage of deer infected with ≥1 worm) and intensity (mean number of worms per infected deer) of *Parelaphostrongylus tenuis* in yearling and adult white-tailed deer collected from Maine during all seasons as related to deer density, 1988 and 1989. Data on deer densities from Maine Department of Inland Fisheries and Wildlife.

were the age class that differed. Prevalence in fawns by sex and year also was analyzed with the general linear model. Prevalence was higher in fawns collected in fall 1988 (66%, n = 87) than in 1989 (23%, n = 73, χ^2 = 28.5, 1 df, $P < 0.001$) (Table 1).

Intensity increased with age class of deer (F = 3.34, 2 df, P = 0.036); no other variables, nor interactions, were significant (Table 2). When fawns were omitted from the data set, age was no longer significant (F = 1.77, 1 df, P = 0.184). Neither prevalence (Rho = 0.038, n = 17, $P > 0.50$) nor intensity (Rho = 0.045, n = 17, $P > 0.50$) was associated with deer density (Fig. 1).

TABLE 2. Intensity of *Parelaphostrongylus tenuis* infections (mean number of worms per infected deer) in white-tailed deer collected in Maine during the fall by age and sex, 1988 and 1989.[a]

Age	Sex	$\bar{x}$ ± SD (*n*)[b]	Maximum
Fawn	Male	2.4 ± 1.4 (34)	10
	Female	2.7 ± 1.8 (38)	11
Yearling	Male	3.6 ± 2.8 (92)	15
	Female	3.5 ± 2.5 (73)	14
Adult	Male	4.2 ± 3.4 (18)	13
	Female	4.2 ± 3.4 (194)	27

[a] Fall 1988 = 30 October to 26 November 1988; Fall 1989 = 28 October to 25 November 1989. Data not significantly different by year (F = 0.168, 1 df, P = 0.682), therefore only pooled means are reported.

[b] Mean number of worms per infected deer ± standard deviation (number of deer sampled).

Heads and fecal samples from the same individuals (n = 42) provided prevalence estimates of 73% and 44%, respectively. Sixteen deer (38%) had worms in crania but did not have larvae in their feces. Four deer (10%) had larvae in their feces, but no adult worms in their crania. Longissimus dorsi (backstrap) muscles were available from three of four deer with feces positive for larvae and were examined for *P. andersoni*, a closely related nematode known to infect deer (Prestwood, 1972); *P. andersoni* was not found.

Prevalence of *P. tenuis* in yearling and adult deer by Biological Zone was not different (χ^2 = 8.91, 7 df, P = 0.27) between this study and that of Gilbert (1973). Also, our intensity data were similar to those of Gilbert (1973). Thus, we concluded no statewide differences in the distribution of *P. tenuis* in Maine were evident between 1968 and 1970 and 1988 and 1989, although variation may have occurred between the two time periods.

TABLE 3. Prevalence of *Parelaphostrongylus tenuis* in yearling and adult white-tailed deer collected in Maine during fall by Biological Zone and time periods.

Biological zone	1968 to 1970[a]		1988 and 1989[b]	
	Male (*n*)	Female (*n*)	Male (*n*)	Female (*n*)
1	83 (24)[c]	91 (42)	73 (15)	86 (28)
2	85 (20)	86 (35)	71 (7)	91 (11)
3	89 (17)	81 (26)	60 (5)	94 (17)
4	83 (39)	83 (83)	85 (40)	86 (109)
5	50 (8)	78 (9)	100 (9)	90 (30)
6	75 (12)	83 (11)	76 (17)	100 (7)
7	58 (24)	80 (35)	94 (18)	85 (33)
8	67 (14)	85 (27)	82 (22)	81 (74)
Overall	76 (158)	84 (268)	83 (133)	85 (309)

[a] From Gilbert (1973, Table 2).
[b] This study.
[c] Percent of deer with ≥1 adult worm (number of deer sampled).

TABLE 4. Intensity (mean number of worms per infected deer) of *Parelaphostrongylus tenuis* in yearling and adult white-tailed deer collected in Maine during fall by Biological Zone and time periods.

Biological zone	1968 to 1970[a]		1988 and 1989[b]	
	Male (*n*)	Female (*n*)	Male (*n*)	Female (*n*)
1	3.7 (24)[c]	4.6 (42)	3.5 (11)	4.7 (24)
2	4.3 (20)	4.4 (35)	3.2 (5)	4.2 (10)
3	5.1 (17)	3.9 (26)	2.0 (3)	2.9 (16)
4	3.8 (39)	4.0 (83)	4.1 (34)	3.8 (94)
5	1.5 (8)	5.3 (9)	3.9 (9)	4.4 (27)
6	3.6 (12)	4.3 (11)	4.2 (13)	5.7 (7)
7	2.5 (24)	3.1 (35)	3.6 (16)	4.0 (28)
8	3.4 (14)	2.4 (27)	3.1 (18)	3.9 (60)
Overall	3.6 (158)	3.9 (268)	3.7 (109)	4.0 (266)
SD	NA[d]	NA[c]	2.9	3.2

[a] From Gilbert (1973, Table 3); sample sizes not given in Gilbert's Table 3, so we assumed the same sample sizes as in his Table 2.
[b] This study.
[c] Mean number of worms per infected deer (number of deer sampled).
[d] Not available from Gilbert's (1973) data.

DISCUSSION

The prevalences of *P. tenuis* in Maine fawns collected in 1967 (66%, $n = 50$, Behrend and Witter, 1968), 1968 (44%, $n = 34$), 1969 (53%, $n = 70$), and 1970 (42%, $n = 51$) (Gilbert, 1973) were not significantly different ($\chi^2 = 1.77$, 2 df, $P = 0.42$). In contrast, prevalence of fawns collected in 1988 (66%, $n = 87$) and 1989 (23%, $n = 73$) did differ ($\chi^2 = 28.5$, 1 df, $P < 0.001$) (Table 1). Because migrating fourth-stage larvae and subadults take about 50 days to reach the cranium, and infections become patent in about 90 days (Anderson, 1963), fawns examined in November must have acquired infections during spring and summer. Evidently, environmental factors affecting transmission of the parasite were different during the growing seasons of 1988 and 1989. July 1989 was cooler by 1 C and had 40% less precipitation than normal (National Oceanic and Atmospheric Administration, 1989). The unusually dry and somewhat cooler July conditions may have slowed development of larvae in gastropods, resulting in reduced prevalence of fawns born in 1989. Also, July weather could have forced gastropods to aestivate, reducing their likelihood of being ingested by deer. Also, unusually deep ground frost in the spring of 1989 caused by relatively little snow cover during winter of 1988–89 (pers. obs.) could have had debilitating effects on gastropod or first-stage larvae populations.

Adult metastrongyloid worms live up to 4 yr (Halvorsen and Hansen, 1985); hence, once a deer is infected with *P. tenuis*, it probably remains infected for a number of years. Based on a lack of annual differences in either prevalence or intensity of *P. tenuis* in yearling versus older deer, we suggest that these infections are a cumulative effect of transmission environments over time. In contrast, prevalence and intensity of infection in fawns result from the transmission environment during one growing season (spring through fall). Thus, annual differences in fawn prevalence might be useful in monitoring annual transmission of *P. tenuis*.

Prestwood and Nettles (1977) found that deer develop an active immunity and resist experimental re-infections of *P. andersoni*, thereby limiting the number of worms per animal early in life. From the similarity in mean numbers of *P. tenuis* from adult deer obtained during the falls of 1988

and 1989, we infer a similar immune response against meningeal worms. Note that mean numbers of *P. tenuis* we found in adult deer (range of means: 3.5 to 4.2) were similar to means found by other researchers [$\bar{x}$ = 3.9, n = 70 (Anderson, 1963); $\bar{x}$ = 3.4, n = 226 (Dudak, 1964); $\bar{x}$ = 3.6, n = 425 (Gilbert, 1973)]. Occasionally, numerous worms are found in a deer, such as the 27 worms we observed in one deer. This may result from failure of the individual's immune system to combat re-infections, or an unusually large number of larvae in an initial infection. Venous sinuses were occluded by masses of worms in approximately 30 deer we examined. Thus, the possibility that adult *P. tenuis* may have debilitating effects in deer, also suggested by Gilbert (1973), should be studied.

We found a *P. tenuis* prevalence of 73% in the deer crania, but only 44% with a Baermann analysis of fecal samples from the same deer (n = 42). Four animals with larvae in their feces for which no adults were found may have had *P. tenuis* in their heads that we simply failed to find, or on spinal cords, which were not examined. In a related study, backstraps from 39 deer were examined for *P. andersoni*; no adult *P. andersoni* or lesions were found (Bogaczyk, 1992). Similarly, 76% (n = 679) of all deer heads we examined were infected with adult *P. tenuis*, while a concurrent MDIFW study using Baermann analyses of deer feces gathered throughout Maine (also using sterilized glassware), 1988 and 1989, provided a prevalence estimate of 46% (n = 723, M. McCollough, pers. comm.). These findings are similar to Upshall et al. (1987), who reported *P. tenuis* prevalence rates of 60% (n = 60) from cranial and 49% (n = 91) from fecal examinations of deer.

Lower prevalence estimates from fecal examinations can be partly explained by the fact that *P. tenuis* is unisexual and thus at least one adult worm of each sex must be present for reproduction. Nine percent of deer we examined had only one adult worm, and assuming no other adults were present, fecal samples from these deer would be negative. Also, assuming a 1:1 sex ratio of worms, 50% of deer infected with two worms would not result in patent infections, 25% infected with three worms would not reach patency, and so on. While prevalence estimates from heads must be interpreted as minimal estimates because of difficulty in finding adult worms, we suggest that estimates from fecal samples will be substantially below the true value. Additionally, at least five species of metastrongyloid parasites known to infect cervids produce dorsal-spined larvae indistinguishable from one another under the light microscope (Pybus and Samuel, 1981). Thus, low prevalence and difficulty in identifying larvae make results of the fecal technique questionable.

Moose populations have expanded in northern and western Maine, largely resultant from extensive clearcutting that increased forage in the 1960's through 1980's, and suspension of hunting between 1936 and 1979 (Morris, 1986). In contrast, deer herds in these two regions of Maine declined during the 1960's and 1970's, and increased through the 1980's (now at 1.5 to 3.5 deer/km^2) (Maine Department of Inland Fisheries and Wildlife, 1991). If the infection parameters for deer measured in this study had been significantly lower than those reported two decades earlier by Gilbert (1973), it could be argued that reduction of moose mortality from *P. tenuis* allowed moose populations to increase. However, we determined that *P. tenuis* prevalence and distribution in deer in Maine in the late 1980's were similar to the late 1960's.

Nudds (1990) suggested that data documenting wide-spread mortality of moose from parelaphostrongylosis does not exist, and that many authors supporting this thinking were guilty of retroductive reasoning. The scenario seen in Maine, where moose populations have increased in spite of presence of white-tailed deer infected with brainworm, does not lend itself to the thinking that *P. tenuis* is a decimating fac-

tor of moose populations. We caution that relationships among deer, moose and *P. tenuis* are extremely complex and should not be viewed in a simplistic fashion, and urge that additional research focus on these interactions to determine effects of *P. tenuis* on moose populations living in areas where *P. tenuis* is endemic.

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