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Parelaphostrongylus tenuis (DOUGHERTY) IN MAINE: I — The parasite in white-tailed deer *(Odocoileus virginianus,* Zimmerman)[1]

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Abstract: Annual prevalence of *Parelaphostrongylus tenuis* for white-tailed deer in Maine varied from 63 to 80 percent during 1968-70. Prevalence was significantly lower ($P<.01$) in fawns than older deer. Adult females had a significantly higher ($P<.01$) prevalence of *P. tenuis* than adult males. Females also had a slightly greater average number of *P. tenuis* per infected animal. An area of relatively low deer density had the highest overall prevalence (81.2 percent), while a region of relatively high deer density had the lowest (59.1 percent).

P. tenuis was most frequently found in the tentorium cerebelli, the falx cerebri and the dura mater. No significant differences in distribution were noted in deer of various sexes and ages. However, 2 percent of the *P. tenuis* found in does apparently had penetrated the neural parenchyma of the brain.

INTRODUCTION

Parelaphostrongylus tenuis, is now well recognized as the etiological agent of neurologic disease in moose.[1,2,4] The white-tailed deer is the usual definitive host of this parasite and does not exhibit the neurologic disorders seen in moose and other cervids.[2] Behrend and Witter[6] reported a high prevalence of *P. tenuis* in deer from Maine. These authors suggested, as did Karns[11] in a Minnesota study, that in areas where deer and moose ranges overlap the density of the moose population might be inversely proportional to the deer population. This suggests that the parasite, and the influence it might have on moose, would be dependent on the density of white-tailed deer. Karns[11] in Minnesota, and Behrend and Witter[6] in Maine have presented evidence that seems to give credence to this argument.

The exact relationship between deer, moose and parasite population densities may, however, be dependent on more complex ecological interactions. The degree of ecological separation between deer and moose population[5,12,15] and not the density of deer may be an important determinant of the influence of *P. tenuis* on moose numbers.

This paper represents the first step in a study to determine the inter-relationships which exist between *P. tenuis* and its definitive and intermediate hosts in Maine.

MATERIALS AND METHODS

Most deer heads examined were collected from meat lockers and cooperating hunters during October - November of 1968, 1969, and 1970. Heads were kept frozen until examined. The presence or absence of adult *P. tenuis,* the number of worms per head, and the location of the worms were recorded for each specimen.

In 1968, areas in the cranial cavity designated for location records were: (1) the blood sinuses lateral to the pituitary (cavernous sinus), (2) the dura mater covering the cavernous sinus (diaphragm sellae), (3) the dura mater lying in the longitudinal fissure between the two cerebral hemispheres (falx cerebri), (4) the dura mater forming the septum between the cerebrum and cere-

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bellum (tentorium cerebelli) and (5) the dura mater not associated with the preceding. Data were recorded as to whether the worms were penetrating into or lying on the surface of the dura. In cases where the cavernous sinus, falx cerebri, or tentorium cerebelli were involved, worms were recorded as lying on, or in, the sinus or folded dura tissues. Based on the 1968 results, the description of nematode locations for 1969 and 1970 was simplified to (1) the subdural space (2) the subarachnoid space, (3) the pia mater and (4) the neural parenchyma.

Age of the deer was determined by tooth eruption, replacement and wear as described by Severinghaus[14] for the 1968 sample, but by tooth eruption and replacement and cemental annuli[10] for the later samples.

Data were tabulated and summarized by sex and age classes and by ecological region of the State. Eight Biological Zones delineated for Maine on the basis of ecological characteristics (Fig. 1) were sampled at some time during the 3 year study. A description of each Zone and the general deer and moose densities for that region follows:

Zone 1:

A mixture of intensive agriculture (primarily potatoes) and spruce-fir woodland. Maple-beech-birch and aspen-birch associations occur to a lesser extent. It lies in the northern climatic zone[9] and is characterized by lacustrine soils and soils that have high lime content. Soils are predominantly channery loams. Deer density is about 3/square mile and moose density 1/square mile.[3]

Zone 2:

Predominantly wilderness and including the largest undeveloped tract of land in Maine. The basic forest type is spruce-fir but the same associations occur as in Zone 1. It also lies in the northern climatic zone, but basic soils are shallow, stony and sandy loams. Deer density is about 5/square mile and moose density about 1.5/square mile.

Zone 3:

Similar topographically and climatologically to Zone 2, but differing in land use patterns, particularly in the developing intensive recreational use. Most of the region is woodland and includes the transition zone between the spruce-fir forests of Zones 1 and 2 and the white pine-northern hardwood forests of Zones 7 and 8. The major forest type is maple-beech-birch. Deer density about 3/square mile and moose density about 0.5/square mile.

Zone 4:

Characterized by the diversity of its land-use patterns which vary from intensive agriculture to commercial woodlands and recreation. Spruce - fir and maple-beech-birch, are the predominant forest types. The area falls in the intermediate climatic zone and the soils are developed in glaciofluvial and marine deposits. Deer density is about 7/square mile and moose density less than 0.1/square mile.

Zone 5:

Almost completely forested by spruce-fir growth and the northern hardwood associations previously mentioned. The soil types are similar to those for Zone 2 and the area falls in the intermediate climatic region. Deer density is about 4/square mile and moose density about 0.2/square mile.

Zone 6:

Subdivided by the coastal climatic region. Land use patterns are variable and the topography is characterized by rough ridges, numerous hills and a relatively large plain area in the east. Aspen-birch, spruce-fir and maple-beech-birch forest

[3] Deer and moose densities are averages for the total Zone area based on 1970 census data for the two species. It should be kept in mind that large differences may exist between specific regions within any Zone.

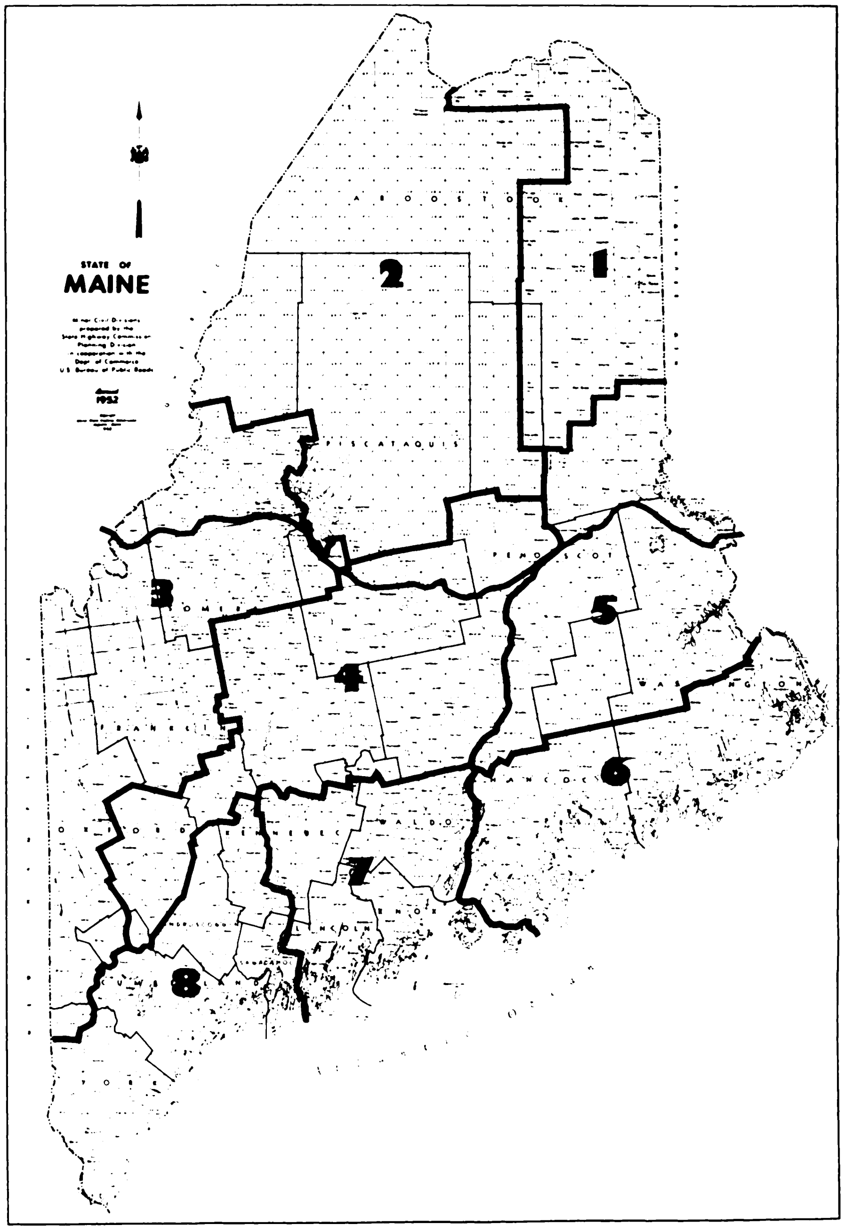

FIGURE 1. Biological Zone map for Maine. (The east-west line extending beyond the state's boundaries represents the division between deer hunting zones).

types are equally predominant. Deer density is about 5/square mile and moose density about 0.1/square mile.

Zone 7:

Supporting a mixed agriculture, semi-urban type of development. A transition of forest types similar to that described for Zone 3 occurs here, although the maple-beech-birch type is not as extensive. Deer density is about 10/square mile and moose density less than 0.1/square mile.

Zone 8:

With the most dense human population (40/sq. mile) of any zone. The area supports white and red pine primarily, but hardwoods are well distributed throughout. Climatic conditions are more moderate than in the other zones. Much of the region is a coastal plain, but the soils are similar to those in Zone 7 (stony, sandy loams, low in silt and clay). Deer density is 10-15/square mile and moose density less than 0.1/square mile.

RESULTS

In 1968, 117 deer heads were examined and 80 percent contained adult *P. tenuis* in the cranial cavity. Of the 269 deer heads examined in 1969, 76 percent were infected and 63 percent of the 1970 sample of 221 heads had meningeal worms. Fawns had a consistently lower ($P<.01$) prevalence of *P. tenuis* than older deer (47.6 vs. 81.0 percent). The percent occurrence of meningeal worm in fawn and adult deer was variable from year to year; adults showed a decline from 1968 through 1970 (Table 1). The number of worms per infected deer also varied annually with 1968 being the high year for adults and 1970 for fawns.

Female fawns had a slightly higher prevalence of *P. tenuis* than male fawns ($P<.50$). However, the difference between adult females and males was highly significant ($P<.01$; chi-square = 11.58). Although females tended to have more nematodes per infection than males (2.24 vs. 2.05 in fawns and 3.93 vs. 3.78 in adults) none of the differences was significant. The older age classes (4½ and 5½+) had fewer worms per infected animal than any of the younger adult classes (males 3.11 vs. 4.60 and females 3.40 vs. 4.43).

Analysis of the data by ecological region indicated that the highest prevalence of *P. tenuis* infected deer was not necessarily related to areas of highest deer density. Biological Zone 2, an area of low deer density, had the highest overall prevalence (81.2 percent) while the value for Zone 7 (59.1 percent) was the lowest despite the high deer densities there (Table 2). Annual changes in infection rates were evident. Despite the small sample sizes it was apparent, for example, that an increase in prevalence of *P. tenuis* in adult male and female deer occurred between 1968-1969 and 1970 in Zone 4. In terms of average numbers of worms per infected animal, the highest loads (4.00+) in adult deer occurred in the lower deer density areas, Zones 1-3 and 6 (Table 3).

The 1968 sample showed the most common site for *P. tenuis* location was the tentorium cerebelli followed closely by the falx cerebri and dura mater (Table 4). The nematodes were generally found lying on the dura mater and diaphragm sellae as opposed to lying in or penetrating the cavernous sinus, the tentorium cerebelli and falx cerebri. No differences, due to sex or age of deer, in the distribution of *P. tenuis* within the cranial cavity, were apparent. The most common infection site was the dorsal subdural space (63.1 percent) in adults and the ventral subdural space (51.9 percent) in fawns (Table 5). The nematodes appeared about equally divided between dorsal and ventral surfaces and were usually closely associated with the meninges or blood sinuses. However, over 2 percent of the adult deer had *P. tenuis* that apparently had penetrated the neural tissue of the brain as they were inside the pia mater and at least associated with the arachnoid if not actually within the neural parenchyma.

TABLE 1. Prevalence and average number of **P. tenuis** in fawn and adult Maine white-tailed deer, 1968-70.

Age	Sex	1968 Incidence	1968 Av. Number	1969 Incidence	1969 Av. Number	1970 Incidence	1970 Av. Number	Total Incidence	Total Av. Number
Fawn	Male	52.4	2.09	48.6	1.94	27.6	2.25	43.0	2.05
	Female	30.8	2.00	60.0	1.81	58.6	2.82	54.6	2.24
	All	44.1	2.07	52.8	1.87*	42.4	2.62*	47.6	2.16
Adult	Male	89.7	4.92	80.0	3.08	67.2	3.85	76.7	3.78
	Female	92.9	4.23	84.6	3.70	75.6	3.89	83.5	3.93
	All	91.8	4.46*	82.9	3.49*	72.2	4.07	81.0	3.88

* Indicates significant difference ($P < .01$) between values on same line

TABLE 2. Percent of white-tailed deer examined from Maine infected with meningeal worms, by Biological Zone, 1968-70.

Biological Zone	Age	1968 Male (n)	1968 Female (n)	1969 Male (n)	1969 Female (n)	1970 Male (n)	1970 Female (n)	1968-70 Male	1968-70 Female	1968-70 Total
1	Fawn	—	—	44 (9)	33 (3)	43 (7)	43 (7)	83	91	74
	Adult	—	—	81(16)	96(24)	88 (8)	83(18)	44	40	
2	Fawn	100 (1)	0 (3)	100 (3)	33 (3)	100 (2)	100 (2)	100	38	
	Adult	50 (2)	100 (9)	91(11)	88(16)	86 (7)	70(10)	85	86	81
3	Fawn	60 (5)	50 (2)	50 (2)	100 (1)	—	—	50	75	
	Adult	89 (9)	88(17)	100 (8)	78 (9)	—	—	89	81	78
4	Fawn	47(15)	38 (8)	50(10)	70(10)	20 (5)	38 (8)	43	50	
	Adult	94(16)	93(27)	79(14)	78(37)	78 (9)	74(19)	83	83	71
5	Fawn	—	—	0 (1)	100 (3)	—	0 (2)	0	60	
	Adult	—	—	67 (6)	88 (8)	0 (2)	0 (1)	50	78	61
6	Fawn	—	—	—	100 (2)	0 (2)	100 (3)	0	100	
	Adult	—	—	50 (2)	100 (4)	80(10)	71 (7)	75	83	77
7	Fawn	—	—	38 (8)	36(11)	25 (8)	50 (2)	31	39	
	Adult	—	—	73(15)	81(26)	33 (9)	78 (9)	58	80	59
8	Fawn	—	—	50 (2)	100 (2)	0 (1)	100 (2)	33	100	
	Adult	—	—	67 (3)	83(12)	64(11)	87(15)	67	85	78

TABLE 3. Average number of **P. tenuis** per infected Maine deer by Biological Zone, 1968-70

Biological Zone	Male Fawn	Male Adult	Female Fawn	Female Adult	All
1	1.86	3.70	3.00	4.61	3.97
2	4.50	4.29	1.33	4.37	4.20
3	1.80	5.06	2.33	3.85	3.94
4	1.54	3.80	2.08	4.04	3.54
5	—	1.50	2.67	5.29	3.64
6	—	3.56	2.80	4.30	3.71
7	1.00	2.50	1.20	3.07	2.54
8	2.00	3.40	1.75	2.35	2.55

TABLE 4. Distribution of **P. tenuis** in Maine deer cranial cavities, 1968. (P = penetrating; LO = lying on; LI = lying in).

			Dura Mater		Diaphragm Sellae		Cavernous Sinus	Tentorium Cerebelli		Falx Cerebri	
Age	Sex	N	P	LO*	P	LO*	LI*	P or LI*	LO	P or LI*	LO
½	M	10	1	4	0	4	7	0	1	0	5
	F	5	0	7	0	2	0	0	0	0	0
1½	M	15	0	5	0	15	18	22	6	13	1
	F	8	0	8	0	3	7	1	1	4	4
2½	M	7	1	2	0	3	2	10	1	15	0
	F	33	0	38	2	24	18	25	13	29	7
3½	M	2	0	2	0	2	0	4	0	0	0
	F	3	0	1	0	2	2	7	2	0	1
4½ +	M	2	0	3	0	0	0	1	2	0	0
	F	8	0	9	0	5	3	3	1	4	0
Total	M	36	2(1)**	16(11)	0(-)	24(16)	27(17)	37(25)	10(7)	28(19)	6(4)
	F	57	0(-)	63(28)	2(1)	36(16)	30(13)	36(16)	17(7)	37(16)	8(3)

* These five locations accounted for 88 percent of all worms found in male deer and 89 percent of all worms located in female deer.

**Figures in brackets represent percent distribution.

TABLE 5. Frequency of occurrence and average number of adult **P. tenuis** by location site in the cranial cavity of Maine deer, 1968-70.

	Percent Occurrence				
Site	Fawns (N = 79)	Adults (N = 366)	Male (N = 165)	Female (N = 280)	Av. Number Nematodes
Dorsal Subdural Space	49.4	63.1	56.4	63.2	1.63
Ventral Subdural Space	51.9	52.2	52.7	51.8	1.20
Dorsal Subarachnoid Space	8.9	13.9	13.3	12.9	0.36
Ventral Subarachnoid Space	6.3	9.0	10.3	7.5	0.22
Dorsal Pia Mater	1.3	1.6	2.4	1.1	0.02
Ventral Pia Mater	3.8	1.9	2.4	2.1	0.04
Lying on Nervous Tissue	2.5	2.5	3.6	1.8	0.07
Penetrating Nervous Tissue	0.0	2.2	0.6	2.5	0.03

DISCUSSION

The prevalence levels of *P. tenuis* in white-tailed deer in Maine found in this study differ from those reported by Behrend and Witter.[6] These authors did suggest, however, that the contrast between their results and Karns'[11] in Minnesota, might have been due to "grossly different conditions" prevailing "in different areas and different years". Our results indicate both temporal and distributional differences in prevalence of *P. tenuis* can be expected to occur naturally in white-tailed deer range. These differences are apparently independent of deer densities as evidenced by a high prevalence in deer of Biological Zones 1-3 and 6, areas of low deer density, and lower levels in the denser populated deer range.

Availability of large numbers of suitable intermediate hosts may be important in transmission of the parasite. Behrend and Witter[6] suggested the high infection rates they noted in the fall of 1967 in deer from Maine could have been due to a wet spring and summer. Precipitation for the years 1968-70 was below normal during May and June in all Biological Zones except 1 and 2 (cf. U.S. Climatological Data). If a positive correlation exists between the size of gastropod populations and the amount of ground moisture, the greater availability of intermediate hosts might explain the higher prevalence of *P. tenuis* found in northern Maine despite the lower deer densities. It would also account for the generally reduced prevalence during 1968-70 from that reported in 1967.[6] If annual differences of this nature exist in gastropod populations this would affect the opportunity for transmission and account for the great variation in average *P. tenuis* load per deer age class.

Adult female deer had a significantly higher prevalence of worms than males, suggesting that sex related behavioral differences may predispose does to greater contact with infected intermediate hosts. This may be a result of fawning and utilization of cover types on the summer range different from those used by males. It is to be expected that these cover types may be more productive of gastropods and increase the opportunity for infection. *P. tenuis* numbers per infected deer of either sex were low which may be indicative of host resistance to increasing numbers of nematodes. Only 8 of the 445 infected deer had more than 10 adult *P. tenuis* in the cranial cavity; the maximum number of worms in any deer was 20.

Dudak et al.[7] reported that 68 percent of the *P. tenuis* they observed in deer crania were on the ventral surface. Behrend[5] also indicated a large percentage of the nematodes were associated with the ventral area of the cranial cavity. This study showed that distribution of adult *P. tenuis* appeared to be about equally divided between dorsal and ventral surfaces.

Signs of neurologic disease are rare in deer,[3] although cases of invasion of neural tissue have been reported.[8,13] It was of interest that almost 2 percent of the deer examined in this study had nematodes that had apparently penetrated the neural parenchyma of the brain. Although some post-mortem movement may be a possibility in this and previous studies, it is possible that *Parelaphostrongylus* may play a slightly more significant role in deer, particularly does, than previously supposed.

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