SEASONAL AND ANNUAL CHANGES IN SHEDDING OF *PARELAPHOSTRONGYLUS TENUIS* LARVAE BY WHITE-TAILED DEER IN NORTHEASTERN MINNESOTA

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ABSTRACT: Changes in prevalence and intensity of *Parelaphostrongylus tenuis* larvae in white-tailed deer (*Odocoileus virginianus*) feces were studied over a 9 year period from October 1986 to May 1995. Overall, first-stage larvae occurred in 46% of fecal samples from 1480 known-age deer killed by vehicles in northeastern Minnesota. Prevalence in fawns rose steadily from October to January and remained fairly constant from February to May (47%) as the animals approached one year of age. The overall prevalence was 59% in deer older than one year and did not vary with increasing age. Prevalence in fawns during February to May varied annually. Number of deer-herd days on winter range with ≤20cm of snow before December 31 was the most important predictor of prevalence. Prevalence also was positively correlated with deer population density, mean May-October temperature, and number of days in September with minimum temperature ≥14°C; but it was negatively correlated with total May-October precipitation. Mean number of larvae/g of feces (overall mean = 49.1 ±3.43SE; range = 0.1-1250) was negatively correlated with deer age. More larvae were shed by deer of all ages during February-May than at other times of the year. Mean numbers of larvae in feces of fawns during February-May varied among years and was significantly correlated with deer population density.

Prevalence is an easily measured parameter that may reflect the multifactorial influence of host and habitat on the transmission of *P. tenuis*, but standardized sampling of deer populations is required to reliably estimate it. Because the parasite is long-lived, only prevalence in the fawn cohort will reflect year to year changes in rates of transmission but infections will only be patent in fawns older than about 8 months.

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The meningeal worm, *Parelaphstrongylus tenuis*, commonly infects white-tailed deer (*Odocoileus virginianus*) in eastern North America but is usually asymptomatic (Anderson and Prestwood 1981). Interest in this nematode parasite continues however, because of its ability to cause severe neuropathology in wild moose (*Alces alces*) and a variety of other cervids and bovids (Anderson and Prestwood 1981, Anderson 1992).

Previously, we (Peterson and Lankester 1991) suggested that the prevalence of *P. tenuis* in white-tailed deer is an easily measured parameter that may be useful as a comprehensive index of interactive host and habitat factors that likely determine the parasite's success in transmission. This approach remains useful, but recent information (Slomke *et al.* 1995) suggests the need for more selective and standardized sampling to provide estimates of prevalence that are sufficiently precise to demonstrate temporal variation.

Deer become infected with *P. tenuis* at an early age and develop a concomitant immunity which prevents subsequent establishment of additional worms (Slomke *et al.* 1995). As well, worms acquired in a deer's first or second summer persist, possibly for

life. Therefore, only examination of successive fawn cohorts will detect annual variability in parasite recruitment.

Infections are detected either by examining deer heads for adult nematodes or by using the Baermann technique to collect first-stage larvae in feces. However, at least 4 months must pass from the time an infected gastropod is ingested before adults or larvae can be found. Because most fawns do not become infected until autumn (Peterson and Lankester 1991), only those examined in late winter and spring can be used to verify infections acquired the previous summer and fall. Although material from hunter-harvested deer is readily available in autumn, samples normally will contain a large proportion of fawns and resulting estimates of *P. tenuis* prevalence will be biased low because infections in many fawns will not yet be detectable .

Over the past 9 years, we collected feces from white-tailed deer killed by vehicles along Minnesota Highway 61 (Peterson and Lankester 1991, Slomke *et al.* 1995). The highway traverses the length of a traditional deer wintering area (2 to 3 km wide and 180 km long) adjacent to the shore of Lake Superior in the vicinity of Grand Marais, Minnesota. Deer exist on their summer range at densities of 1.5-4/km^2 (Lenarz 1995, Lankester and Peterson 1996)and migrate up to 30 km, arriving in the wintering area in November and December; the timing and rate of their arrival can vary from year to year. Samples from most vehicle-killed deer were collected from late-November to early April when deer densities in the yarding area were up to 50/km^2. However, some animals resident in the yard throughout summer at a density of 4/km^2 also became casualties (Lankester and Peterson 1996).

In this paper we evaluate 9 years of data on the prevalence and intensity of *P. tenuis* infection in white-tailed deer as revealed by the presence of first-stage larvae in feces. Our primary objectives were (1) to identify age- and/or sex-related differences in annual prevalence and mean intensity of detectable infections and (2) to determine if observed annual and seasonal differences in infection in the fawn cohorts were associated with environmental and/or behavioral factors.

METHODS

Fecal samples were collected from the colons of white-tailed deer killed by vehicles from October 1986 through May 1994 (n=1480)and from an additional 21 fawns in February-May 1995. The latter animals were used to evaluate annual changes in prevalence and intensity). Samples were frozen at -16°C for up to one month before being examined for nematode larvae using the Baermann technique. Larvae were extracted from weighed samples of 15-25 g of feces placed over a single layer of tissue paper in a glass funnel (90 mm top diam.) filled with water. After 24 h, 12-15 ml of fluid 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). Baermann apparati were cleaned by at least 3 repetitions of alternately flushing hot (40 - 48°C) tap water through the funnel and back flushing. Stems of funnels and tubing were scrubbed with cotton or gauze swabs every 3rd or 4th use. New tubing was installed on the funnels at the beginning, and after the 1st 4 years, of the study.

All deer were assumed to have been born June 1. Age in years was determined from eruption and replacement of teeth and by counting cementum annuli. For analysis, deer were assigned to 3 age classes: fawns (age <1 yr., collected June 1-May 31); yearlings (age 1 yr., in their 2nd year of life); and adults (ages 2-16 yr.). Seasonal differences were evaluated for 7 contiguous time periods (June and July, August 1-October 24, October 25-December 15, December 16 - January 31, February, March, and April and May)

selected according to sample size distribution and white-tailed deer breeding season (Ozaga and Verme 1982).

We analyzed prevalence of *P. tenuis* in deer feces by multiple logistic regression (Hosmer and Lemeshow, 1989). Independent effect variables included host sex, age-class (fawn, yearling, adult), sampling period (midpoint of the sampling period, in days since June 1) and their possible interactions. Linearity of the period effect was assessed by inclusion of a quadratic term (Grambsch and O'Brien 1991). Goodness of fit was evaluated by the Hosmer-Lemeshow test and significance of effect variables by application of log-likelihood, chi-squared tests (Hosmer and Lemeshow 1989). In the case of significant age-class x period interactions, separate reduced models were refit by age-class and corresponding predicted vs. observed prevalences were compared graphically.

Associations between prevalence of *P. tenuis* larvae in fawn fecal samples and several environmental predictor variables were assessed by multiple regression and correlation. Since angular transforms are not required for percentages which range between 20% - 80% (Emerson 1991), we analyzed the untransformed data. Candidate independent predictors included number of deer-herd days on winter range with ≤20cm snow before Dec. 31, spring or pre-fawning deer population density (Lenarz 1995), mean ambient May-October temperature, number of days in September with minimum temperature of ≥14°C, and total May-October precipitation.

Computation of the number of deer-herd days on winter range before December 31 with ≤20 cm snow was based on 3 assumptions: (1) deer will dig through up to 20 cm of snow for forage (Shedd 1981),(2) deer migrate to winter range when summer range snow depths exceed 40 cm and severely restricts deer movement (Kelsall and Prescott 1971) and energetic costs of movement become critical (Moen 1976), and (3) if snow depth is <40 cm, deer arrival on winter range occurs throughout late November and December and in this area can be approximated by assuming that 25% increments of the herd arrive every 10 days; *ie.* that 25% of the herd arrives from November 21-30, a total of 50% by December 10, 75% by December 20, and 100% by December 30 (Peterson, personal observation). Therefore, if summer range snow depth is <40 cm and winter range snow depth is ≤20 cm, each day from November 21-30 equals 0.25 deer-herd day, each day from December 1-10 equals 0.50 deer-herd day, etc. Conversely, if summer range snow depth is ≥40 cm and winter range snow depth is ≤20 cm, each day before December 31 is equivalent to 1.0 deer-herd days. When winter range snow depth exceeds 20 cm, any further transmission of the parasite is unlikely and no additional deer-herd days are accumulated.

Precipitation data were obtained from National Weather Service records, Grand Marais, MN. However, because of the moderating effects of Lake Superior at Grand Marais, we used temperature data from an unofficial monitoring station at Poplar Lake, MN, located within the summer deer range, approximately 37 km inland. Estimates of pre-fawning deer population density were obtained from Lenarz (1995).

Intensity of P. tenuis larvae in deer feces was analyzed by multivariable analysis of covariance (ANCOVA) of log-transformed intensity data. Discrete effect variables included host sex and age-class, while sampling period was treated as a continuous-time covariate. Interaction and linearity of the period effect were evaluated as per the logistic regression analysis (Neter *et al.* 1990). In the case of significant age-class x period interactions, reduced models were refit by age-class, and corresponding predicted vs. observed densities were compared graphically.

Pearson chi-square tests and t-tests were

used to identify annual differences in prevalence and intensity, respectively, of larvae in feces of fawns during the February-May period. Association between intensity of *P. tenuis* larvae in feces of fawns during February-May (dependent variable) and previous spring deer population density (independent variable) was assessed by linear regression.

RESULTS

All recovered dorsal-spined nematode larvae were assumed to be *P. tenuis*. Forty-six percent (n=679) of a total of 1480 white-tailed deer fecal samples contained larvae of *P. tenuis* (Table 1). The earliest patent infection in a fawn was observed October 12, 1988; only 8 additional fawns were patent before mid-December (1986, 2; 1987, 2; 1988, 1; 1991, 2; 1992, 1). Prevalence of larvae in feces of fawns rose rapidly until age 14 months, when it was similar to that found in adult animals.

The full logistic regression model, used to analyze seasonal changes in prevalence, indicated that only age-class (χ^2=29.07, df=2, P<0.0001), period (χ^2=62.13, DF=2,

Table 1. Prevalence of *Parelaphostrongylus tenuis* larvae in feces of white-tailed deer in northeastern Minn., Oct. 1986 - May 1994.

Deer Age Class	Time Period	Prevalence (%) Males		Females		Total	
Fawn	June-July	-	(4)+	-	(2)	-	(6)
	Aug.-Oct.24	-	(21)	6	(16)	3	(37)
	Oct.25-Dec.15	4	(68)	7	(68)	6	(136)
	Dec.16-Jan.	30	(81)	16	(89)	22	(170)
	Feb.	41	(44)	43	(42)	42	(86)
	Mar.	54	(87)	45	(69)	50	(156)
	Apr.-May	50	(26)	40	(20)	46	(46)
	Sub-Total	32	(331)	25	(306)	29	(637)
Yrlg	June-July	47	(15)	80	(20)	66	(35)
	Aug.-Oct.24	42	(19)	43	(14)	42	(33)
	Oct.25-Dec.15	53	(19)	38	(21)	45	(40)
	Dec.16-Jan.	56	(18)	51	(39)	53	(57)
	Feb.	38	(8)	48	(21)	45	(29)
	Mar.	55	(22)	60	(53)	59	(75)
	Apr.-May	67	(6)	73	(26)	72	(32)
	Sub-Total	50	(107)	57	(194)	55	(301)
Adult	June-July	75	(8)	55	(20)	61	(28)
Aug.-Oct.24		40	(5)	61	(31)	58	(36)
	Oct.25-Dec.15	65	(20)	44	(66)	49	(86)
	Dec.16-Jan.	87	(15)	54	(117)	58	(132)
	Feb.	100	(5)	56	(61)	59	(66)
	Mar.	53	(15)	72	(129)	70	(144)
	Apr.-May	100	(3)	70	(47)	72	(50)
	Sub-Total	70	(71)	60	(471)	61	(542)
Total		41	(509)	48	(971)	46	(1480)

+ Number examined in parentheses.

p<0.0001) and their interaction (χ^2=30.29, df=4, P<0.0001) were significant. Therefore, separate temporal regressions were fit, by age-class. Quadratic time models provided the best fit for all age-classes (P<0.01 for all tests of quadratic coefficients). The nature of the interactions is apparent in the age-specific interaction plots (Fig. 1). Prevalence in fawns followed a sigmoid pattern, peaking in late winter and plateauing thereafter; it was relatively stable from February-May, but never equaled that in older deer (overall mean of yearlings and adults = 59%). Prevalence in both adults and yearlings was lowest during late fall-early winter with prevalence in adults generally exceeding that in yearlings.

Comparisons of annual prevalence of larvae in feces of fawns during February-May revealed that prevalence in 1992 was significantly greater than in either 1987 or 1994 (<0.02)(Table 2)but did not differ from other years. Significant environmental predictors of larval prevalence in fawn feces during February-May were number of deer-herd days on winter range with ≤20 cm snow before Dec. 31, mean May-October temperature, and September-October precipitation (see Table 3 for Pearson correlation coefficients).

A multiple regression model containing annual means of number of deer-herd days on winter range with ≤20 cm snow before Dec. 31 and pre-fawning deer population density provided a significant fit ($F_{2,6}$=14.2, P=0.0053) and accounted for 83% of the annual variation of the prevalence of *P. tenuis* larvae in fawn feces during February-May. Squared partial correlations of the two predictors were, respectively, 0.73 and 0.42.

Results of ANCOVA on seasonal changes in larval intensity closely paralleled those of the logistic regression analysis. The full model reduced to one containing age class ($F_{2,678}$=45.14, *P*=0.0003), period ($F_{1,678}$=114.59, P<0.0001) and their interaction ($F_{2,678}$=35.38, *P*=0.0015). Quadratic time period regression models provided significant fits (*P*<0.001) to the fawn and yearling data but a simple linear model sufficed for adults (Fig. 2). Generally, larval intensities differed most among the age classes in summer and spring, converging during the autumn and winter. Maximum intensities in all age classes and both sexes occurred in spring, but while intensities in adults and yearlings continued to rise, the fawn intensity curve began to flatten out after the February collection.

The mean number of larvae/g of feces shed by fawns from February to May was significantly greater in 1992 than in 1994 or 1995 (Table 2). Linear regression revealed significant correlation ($F_{1,136}$=6.15, P=0.0144) between number of larvae/g of feces shed by fawns during February-May and previous spring pre-fawning deer population density. The number of larvae per gram of feces ranged from 0.1 to 1250 and was negatively correlated with deer age (Table 4) but did not differ between the sexes.

DISCUSSION

Increasing prevalence of infection in fawns was associated with the number of deer-herd days spent on winter range, before snow depth exceeded 20 cm,. This probably indicates an extended period for transmission into late November and early December with fawns continuing to access food close to the ground. Gastropods can be active in some years until early Novemeber in this particular wintering area and were more likely to contain infective larvae of *P. tenuis* than gastropods on summer deer range (Lankester and Peterson 1996). Even with the arrival of snow, deer will dig through up to 20 cm to reach ground foliage (Shedd 1981) and may still risk infection.

A prolonged period of transmission in the fall might also increase prevalence by reducing the proportion of sterile, unisexual infections in deer. Assuming that a concom-

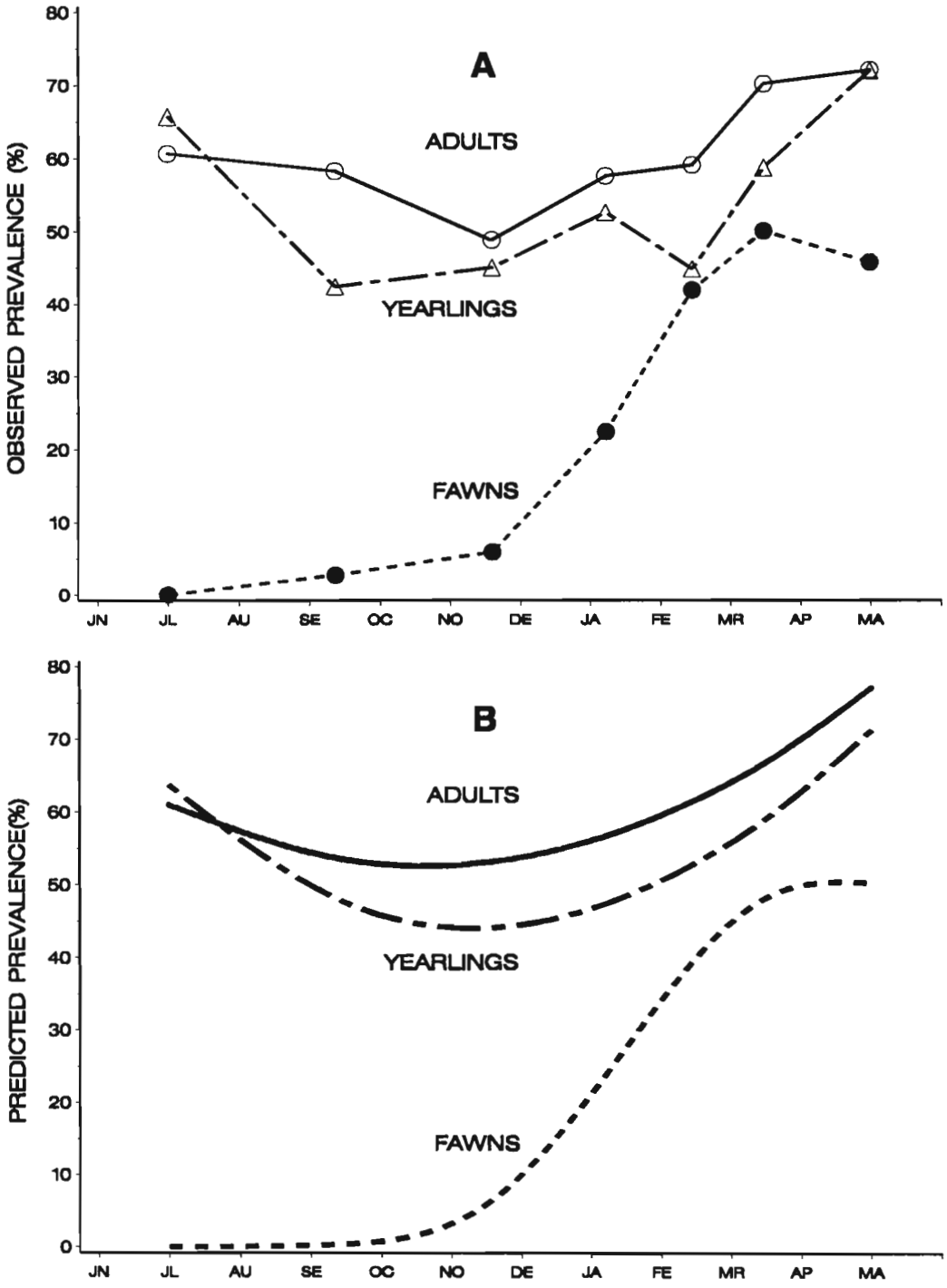

Fig.1. Age-specific seasonal prevalence of *P. tenuis* first-stage larvae in feces of white-tailed deer in northeastern Minnesota, 1986-95. (A) observed prevalence; (B) predicted population prevalence based on logistic regression modelling of observed prevalence.

Table 2. Prevalence and mean number of *Parelaphostrongylus tenuis* larvae /g of feces from infected white-tailed deer fawns (mean intensity) examined during February - May of each year, 1987 - 1995, and selected variables measured the preceding calendar year.

Year	Larvae / g of feces: Prevalence	Mean	SE	Number of deer-herd days on winter range with <20cm snow before Dec. 31	Deer population density (/ sq. km)	Mean May - October temperature (°C)	Number of days in September with minimum temperature ≥14°C	Total May - October precipitation (cm)
1986				6.50	1.9	12.4	0	50.9
1987	35 (37)+a*	75.4	18.56	25.00	2.1	13.0	1	53.0
1988	49 (49)	95.2	35.77	14.25	2.4	13.6	2	56.7
1989	47 (62)	126.3	43.98	19.00	2.1	13.1	3	46.4
1990	53 (15)	65.5	35.55	14.25	2.3	12.2	0	43.6
1991	50 (10)	46.2	23.03	36.00	2.4	13.9	3	42.0
1992	64 (44)a,b	132.2c,d	25.94	19.00	1.8	12.2	1	46.9
1993	41 (29)	77.7	19.52	0.50	1.7	12.0	0	50.9
1994	38 (42)b	51.8c	14.34	25.00	1.5	13.8	4	37.0
1995	48 (21)	30.4d	8.70					

+ Number examined in parentheses.

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

Table 3. Correlations between prevalence of *Parelaphostrongylus tenuis* larvae in feces of white-tailed deer fawns during February-May of each year and variables measured the previous summer-fall.

Variable	Correlation coefficient	Significance level (P=)
Deer-herd days on winter range with ≤20 cm snow before Dec. 31	0.835	0.005
Mean May-October temperature (°C)	0.678	0.045
Number of days in September with minimum temperature ≥14°C	0.624	0.072
Deer population density (deer/sq. km)	0.594	0.092
Total precipitation (cm):		
May-October	-0.423	0.257
May-August	-0.620	0.075
September-October	0.667	0.050

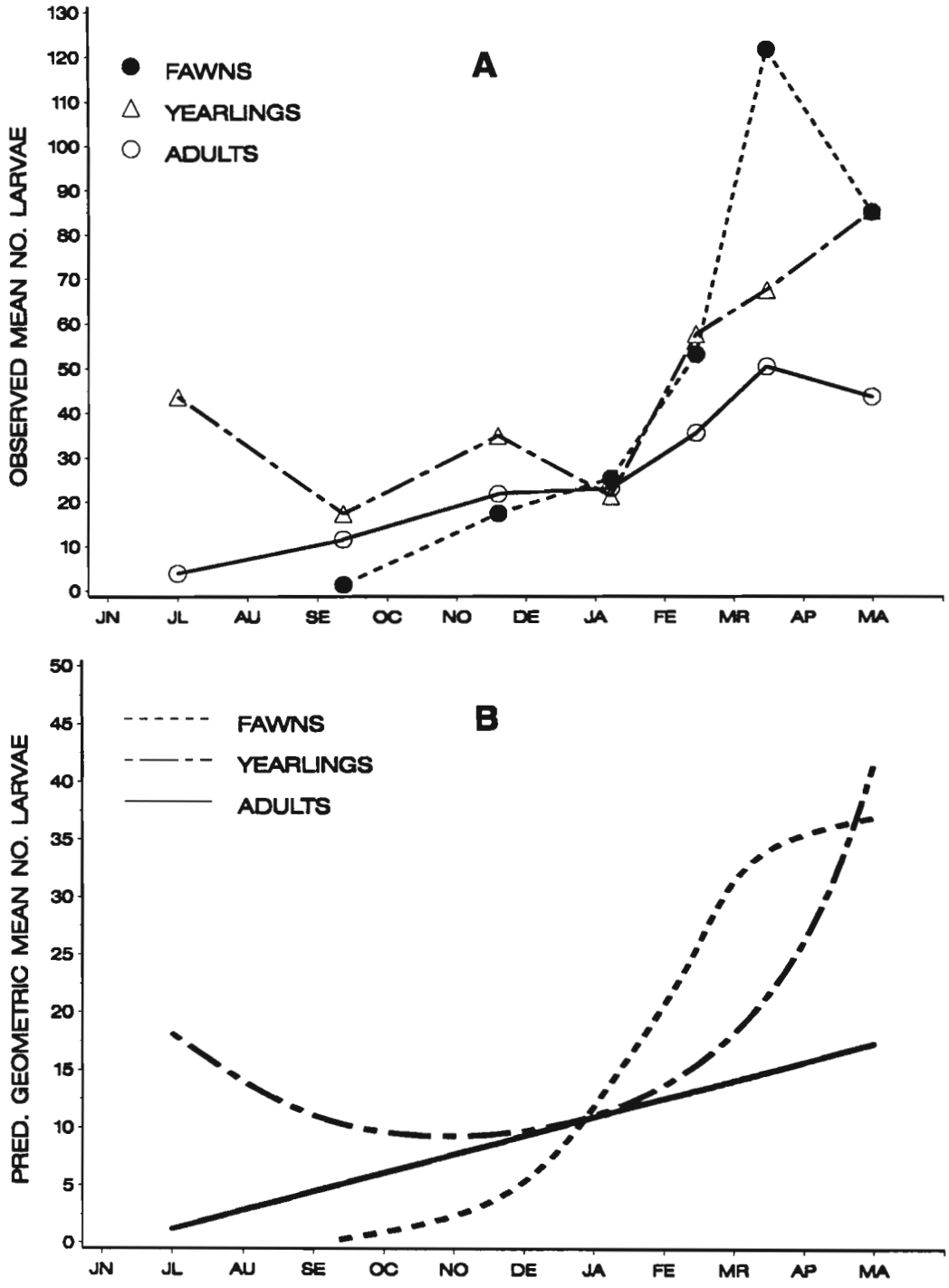

Fig. 2. Age-specific seasonal "intensity" of *P. tenuis* first-stage larvae in feces of white-tailed deer in northeastern Minnesota, 1986-95. (A) observed mean larval intensity; (B) linear model-based predicted geometric mean larval intensity. Geometric means of overdispersed data provide approximations to the underlying population medians (Gilbert 1987) and are thus smaller than the observed means.

Table 4. Mean number of *Parelaphostrongylus tenuis* larvae per gram of feces from infected white-tailed deer (mean intensity) in northeastern Minn., Oct. 1986 - May 1994.

Deer age class	Time period	Number of Larvae / g					
		Males*		Females*		Total*	
		Mean	SE	Mean	SE	Mean	SE
Fawn	June-July	-	-	-	-	-	-
	Aug.-Oct.24	-	-	1.3	-	1.3	-
	Oct.25-Dec.15	26.6	25.91	11.7	10.39	17.3	10.86
	Dec.16-Jan.	24.7	4.58	25.7	13.10	25.1	5.52
	Feb.	55.9	15.59	49.8	20.40	52.9	12.66
	Mar.	103.2	26.88	148.9	32.30	121.3	20.69
	Apr.-May	81.7	32.09	89.7	40.03	84.7	24.43
	Sub-Total	72.3	13.28	86.4	4.98	78.2	10.14
Yrlg	June-July	34.0	20.26	47.8	23.70	43.6	17.38
	Aug.-Oct.24	13.9	6.80	21.6	10.26	17.2	5.72
	Oct.25-Dec.15	34.4	16.65	35.0	12.85	34.7	10.57
	Dec.16-Jan.	14.1	5.43	24.6	10.72	21.1	7.36
	Feb.	65.5	10.58	55.0	19.47	57.4	14.99
	Mar.	64.9	21.67	68.2	11.79	67.3	10.29
	Apr.-May	97.8	74.51	82.3	22.14	85.0	21.55
	Sub-Total	40.8	8.61	53.7	6.89	49.5	6.66
Adult	June-July	5.9	2.70	2.9	1.28	3.9	1.27
	Aug.-Oct.24	3.4	0.65	12.3	6.53	11.5	5.92
	Oct.25-Dec.15	31.0	11.63	17.5	3.85	21.7	4.49
	Dec.16-Jan.	27.1	13.31	22.1	5.65	22.9	5.18
	Feb.	38.1	30.36	34.9	7.31	35.3	7.28
	Mar.	51.3	13.03	50.0	7.34	50.1	6.81
	Apr.-May	23.0	17.66	45.2	12.21	43.3	11.29
	Sub-Total	29.4	5.99	33.7	3.32	33.0	2.99
Total		53.9	7.27	47.0	3.06	49.1	3.43

* Sample sizes can be calculated from data in Table 1.

itant immunity does not develop in fawns until late winter, protracted recruitment of worms might result in more bisexual, patent infections. Slomke *et al.* (1995) found that as many as 30% of infected adult deer had only one sex of worm present. Such infections are not detected by examining feces for larvae.

The highest prevalence of infection in February-May fawns was observed in 1992. Weather conditions the previous autumn clearly provided an opportunity for an extended period of transmission at a time when deer occupied an area with increased likelihood of infection. An unusually early and heavy snowfall on 1 November precipitated an early migration of deer to the winter yard. However, within a few days the snow had melted from most of the south-facing slopes and daytime temperatures remained above freezing through November 22, permitting deer to continue foraging within the yard on fallen leaves and other vegetation low to the

ground.

Pre-fawning deer population density was the only other important predictor of prevalence in fawns in the multiple regression analysis, but was not significant when treated as a single factor (P=.092). Peterson and Lankester (1991) excluded deer density as a reliable predictor of prevalence based on single factor analysis of 4 years of data from the Grand Marais wintering population (1986-91). Other workers, using a variety of sampling methods, have failed to find a consistent correlation between prevalence of *P. tenuis* infection and deer population density (Karns 1967, Behrend and Witter 1968, Gilbert 1973, Thomas and Dodds 1988, Bogaczyk 1990, Garner and Porter 1991, Bogaczyk *et al.* 1993). Standardized sampling, using only fawns collected in late winter, is required for a more thorough investigation of the relationship between prevalence and deer density.

Mean summer-fall temperature had a significant positive univariate correlation with prevalence in the present study, but was not significantly correlated after adjusting for confounding interaction with the other predictors in the multiple regression analysis. The influence of summer temperature on development of third-stage larvae was considered the most important factor affecting transmission of *Elaphostrongylus rangiferi* to reindeer (*Rangifer tarandus tarandus*) in Norway (Halvorsen and Skorping 1981, Handeland and Slettbakk 1994). Possibly, adequate summer temperatures for larval development exist for a shorter period in northern Norway (mean June through August temperature = 11.9 °C; Handeland and Slettbakk 1994) than in northeastern Minnesota (mean May through October temperature = 12.9 °C during this study).

We found the correlation between total precipitation during May-October and prevalence to be negative but nonsignificant while precipitation in September-October was positively correlated. Although these conflicting analyses reduce confidence in the likely importance of precipitation in determining prevalence in the fawn cohort, greater transmission in wetter autumns with delayed cold weather and snow, is consistent with our other findings. Positive correlation between summer precipitation and prevalence of *P. tenuis* in deer has been reported by others (Gilbert 1973, Brown 1983, Bogaczyk 1990, Peterson and Lankester 1991, Bogaczyk *et al.* 1993). In particular, Peterson and Lankester (1991) suggested that the low prevalence in yearling deer in the Grand Marais area in the winter of 1986-87 may have resulted from an unusually dry summer, and presumed poor conditions for gastropods, two years previous. At that point in the study, however, no analyses of meteorological data were done. Handeland and Slettbakk (1994) believed that increased summer precipitation was responsible for outbreaks of cerebrospinal elaphostrongylosis (caused by *Elaphostrongylus rangiferi*) in reindeer. Nonetheless, because of our conflicting results, we recommend further study of the role of summer-fall precipitation in determining the annual prevalence of *P. tenuis* in the fawn cohort.

Nine years of data analyzed here reinforce our earlier conclusion that the number of *P. tenuis* larvae shed decreases with increasing age of deer (Peterson and Lankester 1991, Slomke *et al.* 1995). Lankester and Hauta (1989) made a similar observation for *P. andersoni* larvae passed by caribou (*Rangifer tarandus caribou*). Lower mean numbers of *P. tenuis* larvae from older deer may reflect decreased fecundity of older worms and/or suppression of eggs and first-stage larvae by an increasingly effective immune response (Slomke *et al.* 1995). Anderson (1963) proposed that high larval output by fawns reflected recent infection in immunologically naive animals.

Regardless of deer age or sex, rates of

larval shedding were highest during late winter and spring (February-May). A similar seasonal pattern has been reported previously for *P. tenuis* (Peterson and Lankester 1991, and Slomke *et al.* 1995) and for other elaphostrongyline nematodes (Samuel *et al.* 1985, Lankester and Hauta 1989). Halvorsen *et al.* (1985) observed a yearly cycle of *E. rangiferi* larval output that differred between male and female reindeer. Peaks occurred when the immune response was thought to be lowered by stress; during the fall rut period for males and late winter/spring pregnancy and calving for females. In the present study, no rise in *P. tenuis* larvae was evident in males from October 25- December 15, which is the rut period of white-tailed deer (Ozaga and Verme 1982).

Our observed correlation between larval shedding by fawns and deer population density is difficult to explain and deserves further study. Slomke *et al.* (1995) found greater numbers of larvae shed by deer confined in an area at 30/km^2 than by deer that spent most of the snow-free period at a density of about 2 deer/km^2. Since the mean intensity of adult worms did not differ between the two areas, strain differences in fecundity or a weakened immune response in the crowded deer were suggested as possible explanations. Neither seem applicable in the present study where all deer and their meningeal worms are from the same populations and strain differences are unlikely. As well, the apparent density dependent response is unlikely due to crowding since deer densities during the nine year period remained relatively low at 1.5-4.0 deer/km^2.

Because *P. tenuis* is believed to be long-lived in white-tailed deer (Slomke *et al.* 1995), autumn/winter declines in the prevalence of detectable infections in yearlings and adults was unexpected. However, larval shedding clearly rises and falls throughout the year and, in some individuals, may stop for a period or fall to such low levels that infections can no longer be detected using a limited amount of fecal material and the Baermann funnel technique.

The present work demonstrates the value of long term data sets, particularly in studies where, for the most part, only one data point per variable per year is generated. The potential for shorter term studies to support misleading correlations is apparent if one plots the data in Table 2. For most of the variables listed, there are intervals of two or more consecutive years for which correlations either are nonsignificant or appear the opposite of those supported by data collected over the nine-year period. Clearly, annual variation in biological factors is unpredictable and lengthy study is frequently required to encompass the wide range of possible conditions and to evaluate highly variable, often confounded, interactions (DelGiudice and Riggs 1996).

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