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DISTRIBUTION AND ECOLOGY OF MENINGEAL WORM, *PARELAPHOSTRONGYLUS TENUIS* (NEMATODA), IN NORTHCENTRAL NORTH AMERICA

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ABSTRACT: Meningeal worm (*Parelaphostrongylus tenuis*), a common nematode parasite in white-tailed deer (*Odocoileus virginianus*) and pathogenic for several species of ungulates in eastern North America, is not known to occur in the west. Heads of 1,902 white-tailed deer were examined for adult meningeal worm to determine geographic distribution of the parasite in Saskatchewan and Manitoba (Canada) and North Dakota (USA). Finding the parasite in a deer in eastern Saskatchewan near the Manitoba border established the current northern and western limits in Canada. Prevalence of infection was <1, 18.6, and 8.2% in Saskatchewan, Manitoba, and North Dakota, respectively. Infected deer occurred throughout southern Manitoba and eastern North Dakota. Distribution appears to have changed little since the last published survey for *P. tenuis* in the region in 1972. We examined precipitation, temperature, deer density, and forest cover as likely correlates to prevalence and distribution of *P. tenuis.* Deer management units used for hunting purposes were the scale of analysis in the three jurisdictions. Presence of *P. tenuis* was positively correlated with precipitation during frost-free periods and deer density, and it was negatively correlated with winter and spring temperatures. Landscapes with >25 and <75% forest cover were most likely to have infected deer. Low rainfall and low density of white-tailed deer likely influence the westernmost limit of *P. tenuis.*

Key words: Ecologic correlates, geographic distribution, Manitoba, meningeal worm, North Dakota, *Odocoileus virginianus, Parelaphostrongylus tenuis,* Saskatchewan, white-tailed deer.

INTRODUCTION

Parelaphostrongylus tenuis, called meningeal worm, is a common parasitic nematode of white-tailed deer (WTD; *Odocoileus virginianus*), throughout the deciduous mixed-hardwood forests of eastern North America (Lankester, 2001). It has been reported as far west as western Manitoba (Bindernagel and Anderson, 1972) in Canada and western Nebraska in the United States (Oates et al., 2000). It has not been reported from the boreal mixed-wood forest of northcentral and western Canada characterized by a short growing season and relatively low densities of WTD. Bindernagel and Anderson (1972), Samuel and Holmes (1974), and Shoesmith (1976) expressed concern that *P. tenuis* might be expanding its range westward through the Aspen Parkland Ecoregion, eventually arriving in western North America where WTD occur sympatrically with susceptible ungulate populations.

Objectives of this study were to determine the distribution and westernmost occurrence of *P. tenuis* in white-tailed deer of Saskatchewan (SK; Canada), Manitoba (MB; Canada), and North Dakota (ND; USA) and to correlate the presence of the parasite in WTD from deer management units to four ecologic factors: precipitation, temperature, density of white-tailed deer, and percent land forested.

STUDY AREA

This study encompassed the hypothesized northwestern distributional limit of *P. tenuis* in North America, which includes the Great Plains, aspen parkland, and deciduous and boreal mixed-wood forest regions of SK, MB, and ND. Topographic relief throughout the area is highly varied, ranging from the gentle rolling prairie of southern SK to the precipitous badlands along the Little Missouri River in southwestern ND. Elevation ranges from 200 m above sea level along the Red River Valley in eastern ND and southeastern MB, to 800 m above sea level in the Turtle Mountains of western ND and MB, Duck Mountains of MB, Missouri Plateau of southwestern ND, and the Cypress Hills of southwestern SK.

More important than annual precipitation and average annual temperature in describing the climate of the region is frequency and amplitude of precipitation as well as year-to-year variation in average seasonal temperature. Long term dramatic annual fluctuations in precipitation and frequent wildfires associated with dry periods have greatly influenced vegetation dynamics and associated animal diversity. Average annual precipitation increases west-to-east from southwestern SK to eastern ND. Frost-free periods range from approximately 150 days in the south to less than 110 days in the north. Temperatures range as low as −45 C in January and as high as +40 C in July and August. More descriptive information on the region is in Wasel (1995).

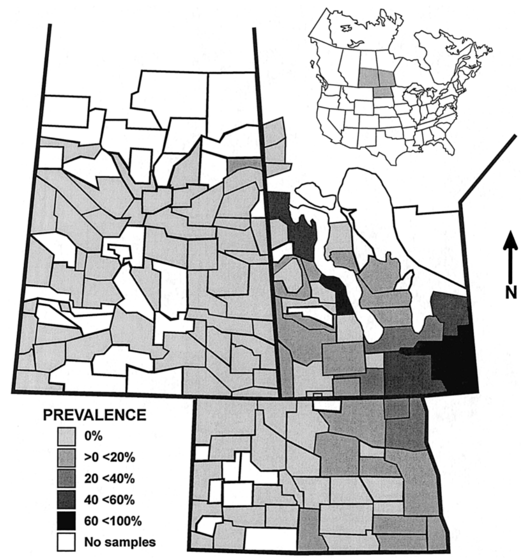

FIGURE 1. Prevalences of *Parelaphostrongylus tenuis* in white-tailed deer arrayed by deer management units in Saskatchewan, Manitoba, and North Dakota. A total of 1,902 deer heads was included in analysis. Map is not to scale.

METHODS

Deer heads were collected from hunters during 1989 and 1990 deer hunting seasons (November) in cooperation with provincial and state fish and wildlife departments, local wildlife branches, wildlife research agencies, local hunting clubs, and meat processing plants. Emphasis was placed on the importance of knowing where deer were killed, at least to deer management unit (DMU) (Fig. 1). The cancelled hunting license was attached to the carcass of all WTD killed during the hunting season in ND. Game agency personnel recorded date of kill and DMU for all deer killed in MB and SK. Heads were stored in freezers or outside (cool or frozen) until transport to Edmonton (Alberta, Canada) where they were frozen pending necropsy.

Sampling protocol was designed to examine deer from as many DMUs as possible. Most heads were collected in 1989 (n=919) and 1990 (n=946), but a few others were available from 1987 (2), 1988 (28), 1991 (1), and year unknown (6). In 1989, deer heads were collected from wherever they were available within the three jurisdictions. In 1990, heads were collected only from DMUs from which <30 heads were examined in 1989. Deer with partial data available were included in all possible analyses. Thus, data from 415 fawns, 617 yearlings, 859 adult, and 11 unsexed deer from known DMUs were included in the distribution map (Fig. 1).

All WTD heads with antler pedicels on the frontal bones were classified as male. Deer were classified as fawn, yearling, or adult based on patterns of mandibular tooth eruption and wear (Severinghaus, 1949). When an infected deer was discovered that could not be aged accurately based on tooth eruption pattern (n=93), the first incisor was extracted, cleaned, sealed in a clearly marked envelope, and sent for sectioning, staining, and mounting (Matson's Laboratory, Milltown, Montana, USA). The senior author examined mounted slides and age was interpreted based on cementum annuli analysis.

Frozen heads were sagittally sectioned using a heavy-duty bandsaw. The sagittal cut was offset approximately 3 mm from the median plane to reduce the chance of destroying worms within the sagittal venous sinus. The thinnest possible blade (2-mm kerf) was used to minimize the risk of destroying worms during sectioning. Heads thawed overnight were examined for adult *P. tenuis*; both sagittal sections were examined along the surface of the cut. The cerebrum and cerebellum were teased from the meninges and surfaces were inspected visually under bright light. Sulci were probed and each sagittal half of the brain was sectioned (~1 cm intervals) and examined for *P. tenuis* embedded in neural tissue. The olfactory bulb was then teased from the cribriform plate using a scalpel and examined. With the neural tissue entirely removed from the cranium, the surface of the meninges was examined using a dissecting microscope at 6×. Cavernous, transverse, and sagittal sinuses were opened using a scalpel and forceps and examined at 6×. The total number of worms from each head was recorded and all worms were fixed in glycerin alcohol.

A statistical significance standard of $P<0.05$ was used for all tests unless stated otherwise (Sokal and Rohlf, 1981). Parasites were identified using the description of Anderson (1963). A voucher specimen from infected deer from SK is in the University of Alberta Museum of Zoology Parasite Collection (UAPC No11532).

Based on literature on meningeal worm, we chose the following as likely correlates to *P. tenuis* prevalence and distribution: precipitation, temperature, WTD density, and forest cover. We felt that gastropod abundance and distributions were important, but unfortunately few data were available (see Wasel, 1995).

Climate

The finest spatial scale in which prevalence and distribution of *P. tenuis* could be resolved was DMU. Several DMUs contained more than one weather station, while a few had none (Anonymous, 1989a, b). Weather stations were selected on the basis of being most representative of the biogeoclimatic features (i.e., latitude, longitude, elevation, slope, aspect) of a DMU. Of the 169, 286, and 149 climate stations in MB, SK, and ND, respectively, 30, 40, and 31 were selected to represent the 37, 51, and 31 DMUs from which WTD were collected in MB, SK, and ND, respectively.

Climate data between Canadian and USA jurisdictions were kept separate, because preliminary analysis between the southern half of MB and SK (where WTD were collected) and throughout ND revealed that the associated change in latitude had a significant effect on seasonal temperatures and seasonal precipitation. Separate analysis minimized dilution of these discrete differences and avoided confounding effects that pooling climate data between jurisdictions might have had on interpretation of results. Also, there were differences between jurisdictions in methods of collecting and storing data and variability in number of years that data were recorded.

Climatologic data were obtained from the National Climatic Data Center (Asheville, North Carolina, USA) for ND in 1989 and 1990 (Anonymous 1989b, 1990). Climatologic data for MB and SK were obtained from Environment Canada, Atmospheric Environment Service (Anonymous, 1989a). Long-term climate data were determined using 30-yr means for a given area (1951–80) (Anonymous, 1982). The following information was used to determine ecologic associations between 30-yr climate data and presence and prevalence of *P. tenuis*: 1) average daily, monthly, seasonal, and annual precipitation, 2) average daily, monthly, seasonal, and annual temperature, 3) monthly maximum, minimum, and average temperatures, 4) number of days >0 C each month, and 5) number of days precipitation each month. In ND an index of freeze-thaw periods, measured as the number of days below freezing each month, was tested for correlation to DMUs with and without *P. tenuis.*

Prevalence data for *P. tenuis* were compared with climate data on long and short-term temporal scales using 30-yr means and annual climate. For climate to be correlated with presence or absence of *P. tenuis* we assumed that 1) prevalence of *P. tenuis* in a deer population did not fluctuate markedly year-to-year over the 2-yr study period and 2) annual fluctuation in climate did not greatly affect prevalence of *P. tenuis* within the deer population as a whole, but rather long term ecologic conditions are what determined presence or absence of *P. tenuis.* These assumptions are based primarily on the fact that meningeal worm is long-lived in deer (Duffy et al., 2002). Accepting these two assumptions, we pooled prevalence data (age and sex combined) for all DMUs between years and compared prevalence with the 30-yr climate data. All DMUs were grouped according to whether *P. tenuis* was present or absent.

The following parameters were used to test for correlation with the presence of *P. tenuis* within each DMU sampled: mean 30-yr annual temperature; mean seasonal temperature; monthly average maximum daily temperature; monthly average minimum daily temperature; monthly average mean daily temperature; number of days/month below freezing (ND only); mean 30-yr annual precipitation; mean seasonal precipitation; mean 30-yr monthly rainfall; mean 30-yr monthly snow and sleet; mean 30-yr monthly precipitation; 30-yr number of days rain (MB and SK only); 30-yr number of days snow (MB and SK only); and 30-yr number days precipitation. Mean values for each parameter, for all 119 DMUs sampled, were determined for each month. Mean values (±standard errors [SE]) for DMUs with *P. tenuis* present were compared with mean values (±SE) for units without *P. tenuis* using a paired-sample *t*-test (Zar, 1984). A significance of $P<0.001$

was used to determine whether monthly means differed significantly between units with or without *P. tenuis.* Correlation of meningeal worm with the ecologic variables was tested further using univariate and multivariate nominal logistic regression models (SAS Inst., Inc., 1989). These models were used to determine association of each ecologic variable with presence or absence of *P. tenuis* as well as to determine which combinations of ecologic variables were most strongly correlated with presence of *P. tenuis.* For variables with a significant correlation to presence of *P. tenuis,* an attempt was made to define threshold values describing the probability of having meningeal worm present under specific ecologic conditions.

Univariate linear regression analysis was done to determine whether increasing prevalence of meningeal worm was correlated with monthly and seasonal temperature and precipitation. Only DMUs (n=34) with a sample size >1, and with *P. tenuis,* were included in this analysis.

Annual climate was the second temporal scale used to determine ecologic variables associated with presence or absence of *P. tenuis.* For annual climate to have a correlation with presence of *P. tenuis,* we assumed that 1) presence or absence of meningeal worm might change over short periods of time (i.e., <2 yr) and 2) prevalence, especially prevalence in fawns, might fluctuate annually depending on transmission conditions. If transmission of *P. tenuis* is sensitive to annual climate change, it should be manifested year-to-year in parasite prevalence in fawns acquiring the parasite the first time. However, number of fawns sampled from the same DMU for each of 1989 and 1990 was not large enough to allow rigorous statistical testing of the correlation of prevalence in fawns with annual climate. Thus, prevalence data were pooled for fawns, yearlings, and adults. Correlation of presence-absence of meningeal worm in DMUs with annual climate was done using logistic regression analysis.

At a geographic scale broader than DMUs, prevalence data for fawns in each of two regions, southeastern MB and eastern ND, were pooled. Annual prevalence data were then compared with the respective annual climate data (i.e., each management unit, 1989 prevalence compared with 1989 monthly and seasonal temperature, and monthly and seasonal precipitation). The objective was to determine whether annual changes in prevalence were correlated with annual fluctuations in climate.

Other ecologic correlates and potential for establishment elsewhere

Unpublished data on WTD density, obtained from SK, MB, and ND wildlife management agencies, were summarized as deer/km^2. Only DMUs (n=89) with density information were included in analyses. All agencies felt that their deer density estimates had broad confidence limits and only SK was able to provide confidence limits for 20 management units. Because of this, data were pooled in three categories: low (0–0.37 deer/km^2), medium (>0.37–1.1), and high (>1.1). Deer density was then compared with presence or absence of *P. tenuis* using univariate logistic regression analysis.

Land-use information, specifically percent of DMU forested, was determined from computer interpretation of Landsat satellite color photographs supplemented with infrared high-elevation aerial photograph interpretation and land cover associations (Anonymous, 1989c). Because of difficulty discerning shrub types from early successional forest types, late season cultivated crops, or grazed forest lands, and because of the difficulty obtaining digital land coverage data, percent of each deer management unit forested was expressed as four categories: <25%, <50%, <75%, and <100% forested (percent forested=stands of timber >15 m height, with windrows excluded). Each DMU examined for *P. tenuis* was then assigned a category.

As one test of estimating potential establishment of *P. tenuis* in western regions where the parasite is not currently present, suitability of climate for presence of *P. tenuis* in Edmonton (Alberta, Canada; 53°34′N, 113°31′W) was evaluated using the univariate regression models generated by the ND and MB data.

RESULTS

Distribution, prevalence, and intensity of *P. tenuis*

A total of 195 of 1,902 deer (10.2%) from MB (149/799; 18.6%), SK (1/565; 0.2%), and ND (45/538; 8.5%) had *P. tenuis*; most infected WTD were from southern MB and eastern ND (Fig. 1). Prevalences were highest in southeastern MB (percent infection in each of the three easternmost DMUs from which WTD were examined was 53, 67, and 63) and decreased with increasing distance northwest, west, and southwest of this region. High prevalences in southeastern MB decreased to >20 but <60% in DMUs of southcentral MB and for the most part >0 but <20% in southwestern DMUs (Fig. 1). Only three of 126 WTD from the two extreme southwestern DMUs of MB and none of 200 WTD from the four SK DMUs abutting southwestern MB were infected. The westernmost infected deer (an adult female) was killed in eastcentral SK near the town of Cumberland House, about 60km from the MB border (54°N, 102°W).

Numbers of worms present (i.e., intensity) were recorded for 187 of the 195 infected deer. Mean intensity of infection was 2.3 (±1.8 SD), but most deer (125, 67%) had two or fewer worms; 83 (44%) had one worm. Eleven worms were recovered from each of two deer. The infected WTD from SK had one adult male worm.

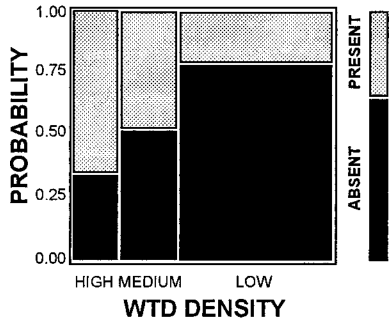

FIGURE 2. Univariate nominal logistic regression of white-tailed deer density versus presence or absence of *Parelaphostrongylus tenuis* for 89 of 119 deer management units sampled in North Dakota, Manitoba, and Saskatchewan. High≥1.1 deer per km^2; medium=0.38–1.1 deer per km^2; low=0–0.37 deer per km^2. Data were not available for 30 deer management units.

Climate (30-yr means)

There was no difference (paired *t*-test) between mean (1951–80) annual or seasonal temperature for DMUs with *P. tenuis* present and absent. Also, monthly means of daily maximum, daily minimum, and daily average temperatures were not significantly different for DMUs with or without *P. tenuis.* There was no significant difference in the number of days below freezing each month in ND DMUs with or without *P. tenuis.*

Annual and seasonal precipitation in summer and fall was higher ($P<0.001$) in DMUs with than without *P. tenuis.* Total monthly precipitation was significantly higher from July through September in ND and from August through November in MB and SK in DMUs with than without *P. tenuis.* Precipitation in the form of snow and/or sleet was not significantly different between DMUs with and without *P. tenuis.* There was no significant difference in number of days with precipitation per month in ND between DMUs with than without *P. tenuis,* but differences were significantly higher for October in MB and SK.

Climate (1989 and 1990)

In ND, there was only one significant difference between DMUs with *P. tenuis,* compared with DMUs without *P. tenuis.* This minimal correlation indicated that further analysis of annual means, using the combined MB and SK data, and its associated lower resolution climate data (fewer climate stations over broader geographic areas), was unrewarding.

There was no difference in the pooled prevalence for all fawns from southeastern MB for 1989 and 1990 (11/116, 9.5%; and 4/35, 11.4%, respectively) in spite of the fact that, of the seven management units for both 1989 and 1990 that had a sample of fawns and corresponding monthly precipitation data, there was higher precipitation for January, February, March, April, May, June, and July at each station (12–25% more) in 1990 compared with 1989. Likewise, there was no difference in the pooled prevalence for all fawns examined from eastern ND for 1989 and 1990 (4/66, 6.1%; and 1/62, 1.6%, respectively) in spite of the fact that spring and summer precipitation, 1990, was 80% of normal and spring-summer temperature was 1.7 C above normal.

Deer density and forest cover

Deer density was significantly correlated with the presence of meningeal worm (Fig. 2). The r^2 value for predicting the presence of *P. tenuis* based on deer density alone was 0.12 ($P<0.001$) with *P. tenuis*

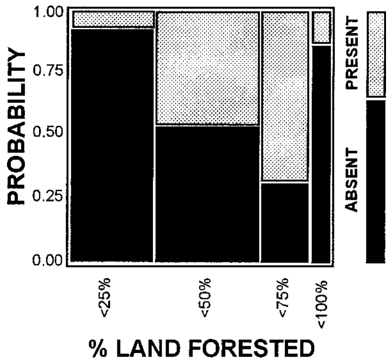

FIGURE 3. Univariate nominal logistic regression of percent forested land versus presence or absence of *Parelaphostrongylus tenuis* for 89 of 119 deer management units sampled in North Dakota, Manitoba, and Saskatchewan. Data were not available for 30 deer management units.

least likely to be present in units with low deer density. In areas of high deer density the logistic regression model predicted that the probability of having meningeal worm present in the deer population was approximately 70%.

Presence of *P. tenuis* was also correlated with forested land (Fig. 3). Absence of *P. tenuis* was most likely in DMUs with <25% of the land area forested; presence of *P. tenuis* was most likely in DMUs >25% and <75% forested (r^2=0.22). In DMUs with between 50 and 75% forest cover, the forest class most likely to have infected deer, the model predicted the probability of having *P. tenuis* present in the deer population was approximately 70%.

Correlation of ecologic variables with presence and prevalence of *P. tenuis*

Logistic regression models: For all DMUs sampled, mean monthly precipitation from March through November and mean monthly temperature from December through February generated significant univariate logistic regression models (P<0.05) (Table 1). As mean monthly precipitation increased, the probability of having *P. tenuis* present within a deer population also increased. Mean monthly temperature for December through February and mean seasonal temperature for winter, was inversely associated with the presence of *P. tenuis*; DMUs with lower mean temperatures had a higher probability of having *P. tenuis* present within the deer population.

TABLE 1. Ecologic variables that generated a significant univariate logistic regression model predicting the presence or absence of *Parelaphostrongylus tenuis* within a deer management unit.

Ecological variables	r^2	P value
Precipitation mean, March	0.06	<0.001
Precipitation mean, April	0.08	0.003
Precipitation mean, May	0.06	0.01
Precipitation mean, June	0.05	0.015
Precipitation mean, July	0.22	<0.001
Precipitation mean, August	0.33	<0.001
Precipitation mean, September	0.21	<0.001
Precipitation mean, October	0.19	<0.001
Precipitation mean, November	0.06	0.007
Temperature mean, December	0.04	0.024
Temperature mean, January	0.04	0.026
Temperature mean, February	0.07	0.02
Precipitation seasonal, Spring	0.13	<0.001
Precipitation seasonal, Summer	0.32	<0.001
Precipitation seasonal, Fall	0.19	<0.001
Temperature seasonal, Winter	0.05	0.014

Deer density, percent forested land, winter and spring temperature, and summer and fall precipitation generated a multiple logistic regression model that explained 57% of the variation in presence or absence of *P. tenuis* (P<0.001) (Table 2). Of all ecologic variables analyzed, the six mentioned above generated statistically significant models and had the highest predictability for the presence or absence of *P. tenuis.* Each was forward and reverse loaded into stepwise logistic regression analysis. Summer precipitation had the single highest contribution followed by spring temperature and percent of DMU forested (Table 2). The multiple regression model generated indicated that the following were the specific conditions within the study area that had the highest correlation with the presence of *P. tenuis*: high summer and fall precipitation, low winter and spring temperature, forest cover between 50 and 75%, and high deer density.

TABLE 2. Ecological variables loaded in multiple logistic regression analysis with corresponding r^2 values ($P < 0.001$).

Ecologic variable	r^2
Summer precip.[a]	0.319
Summer precip./fall precip.	0.338
Summer precip./fall precip./winter temp.[b]	0.343
Summer precip./fall precip./winter temp./spring temp.	0.499
Summer precip./fall precip./winter temp./spring temp./percent forested	0.561
Summer precip./fall precip./winter temp./spring temp./percent forested/deer density	0.572

[a] Precip.=precipitation.
[b] Temp.=temperature.

Linear regression models: Linear regression analysis, including all DMUs within the study area with *P. tenuis* present, revealed no significant correlation between prevalence of *P. tenuis* infections and precipitation or temperature. When data for ND and MB were analyzed separately, winter and fall precipitation for ND was positively correlated with prevalence.

Potential establishment elsewhere

Spring and fall precipitation in Edmonton predicted a 20% and 15% probability, respectively, that *P. tenuis* was present, while the summer precipitation model predicted an 88% probability that *P. tenuis* was present. The summer and fall temperature model was not significant, therefore temperature conditions for Edmonton could not be evaluated.

DISCUSSION

Finding one infected white-tailed deer in eastern SK established the northwestern limits of *P. tenuis* in Canada. The recent finding of meningeal worm in a WTD from western Nebraska (Oates et al., 2000) established the westernmost finding for the United States. Samuel and Holmes (1974) hypothesized that the grassland biome of central North America acts as a barrier to the western spread of *P. tenuis.* This appears to be true, at least in Canada where the westernmost distribution of *P. tenuis* has not changed much if at all from the late 1960s (Bindernagel and Anderson, 1972) to 1990 (present study). Bindernagel and Anderson (1972) found meningeal worm in a white-tailed deer collected approximately 50 km from the SK border in southwestern MB, and no adult worms were recovered from 60 white-tailed deer examined from southeastern SK. In the current study, *P. tenuis* was, with two exceptions (one infected WTD in each of southcentral ND and eastcentral SK), not found in WTD in the high plains of western ND or the Great Plains, Aspen Parkland Ecoregion, or deciduous and boreal mixed-wood forests of SK. Thus, there is no evidence of westward range expansion of meningeal worm via the aspen parklands of southwestern MB and across SK (southeast to westcentral) or via the mixed-wood forests north of the aspen parklands.

In contrast, Oates et al. (2000) suggested that *P. tenuis* has recently spread westward in Nebraska and indicated that the prairie habitat is not a natural barrier to spread of the parasite. They suggested that meningeal worm larvae might survive along rivers, streams, and other wet areas in numbers sufficient to infect deer. This makes our analysis of ecologic factors and presence of meningeal worm, timely.

Correlations of higher summer through fall precipitation, lower winter and spring temperatures, higher deer density, and moderately forested areas with presence of *P. tenuis* infections in white-tailed deer (WTD), make biological sense. Six species of known intermediate hosts of *P. tenuis* were part of a small collection of terrestrial gastropods from southern SK and MB and eastern ND (Wasel, 1995). Terrestrial gastropods "require moisture" (Burch and Pearce, 1990). So too, the free-living first-stage larvae of meningeal worm. Gastropods become relatively inactive when moisture is low (Burch, 1956), and deer feces and surface soil (both with first-stage larvae of *P. tenuis*) become dry. The likely result is increased mortality of *P. tenuis* larvae and curtailed transmission (see Lankester and Anderson, 1968). Beetle (1989) indicated that extremes of temperature, short periods between killing frosts and little moisture likely contribute to fewer gastropods.

Negative correlation of presence of *P. tenuis* with winter temperatures, as revealed by logistic regression analysis, could be related to the ability of first-stage larvae to survive cold temperatures (Shostak and Samuel, 1984). Also, we assumed that DMUs with the coldest monthly temperatures typically have the fewest freeze-thaw cycles and such cycles have been shown to decrease survivorship of first-stage larvae (Shostak and Samuel, 1984). Alternatively, it is possible that correlation between winter temperatures and *P. tenuis* has no ecological significance, but rather may be an artifact of interactions between topography and temperature.

The odds of encounter between an infected gastropod and a WTD depend on density and spatial overlap of each organism within the environment. Gastropod intermediate hosts must have spatial and temporal overlap with infected deer feces or first-stage larvae. High densities of WTD and infected gastropods with an associated spatial overlap between the two, likely enhance transmission. Univariate regression analysis revealed a significant positive correlation between the presence of meningeal worm and high density WTD. The low predictive power between presence of *P. tenuis* and deer density could be related to several factors including low precision of deer-density data provided by the game agencies.

The relationship between presence of meningeal worm and percent forest cover is not surprising given the habitat preference of WTD; i.e., *P. tenuis* can only occur where there are WTD, and WTD prefer habitats with a mixture of abundant forage adjacent to forest cover that provides thermal cover and concealment. In addition to the influence that forest cover may have on WTD, forest cover also likely plays a significant role in moderating microclimate near the forest floor, and, hence, habitat of terrestrial gastropods.

One important question for many jurisdictions west of the apparent ecological barrier of the Great Plains is whether or not *P. tenuis* can establish there. This did not happen when infected WTD from eastern Oklahoma were relocated to western Oklahoma (Kocan et al. 1982). For Edmonton climate, only the summer precipitation model predicted a high percent probability that *P. tenuis* was present.

The positive correlation of presence of *P. tenuis* with precipitation suggests that lower rainfall associated with the prairie biome may act as a natural ecologic barrier for natural westward spread of *P. tenuis.* Historic wildfires that swept across the prairie biome each spring prevented encroachment of trees and shrubs that now provide cover for both gastropods and WTD. Current and extensive cultivation of historic natural grasslands may accentuate the climatic barrier of the grassland biome or at least compensate for the elimination of fire; however, other factors such as irrigation, high deer density, and forest cover may erode what was once a natural barrier.

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