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Source: Journal of Wildlife Diseases, 53(1):131-135.
Published By: Wildlife Disease Association
DOI: http://dx.doi.org/10.7589/2016-02-028
URL: http://www.bioone.org/doi/full/10.7589/2016-02-028

DOI: 10.7589/2016-02-028

*Journal of Wildlife Diseases*, 53(1), 2017, pp. 131–135


# Associations among Habitat Characteristics and Meningeal Worm Prevalence in Eastern South Dakota, USA

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ABSTRACT: Few studies have evaluated how wetland and forest characteristics influence the prevalence of meningeal worm (*Parelaphostrongylus tenuis*) infection of deer throughout the grassland biome of central North America. We used previously collected, county-level prevalence data to evaluate associations between habitat characteristics and probability of meningeal worm infection in white-tailed deer (*Odocoileus virginianus*) across eastern South Dakota, US. The highest-ranked binomial regression model for detecting probability of meningeal worm infection was spring temperature + summer precipitation + percent wetland; weight of evidence ($w_i$=0.71) favored this model over alternative models, though predictive capability was low (Receiver operating characteristic=0.62). Probability of meningeal worm infection increased by 1.3- and 1.6-fold for each 1-cm and 1-C increase in summer precipitation and spring temperature, respectively. Similarly, probability of infection increased 1.2-fold for each 1% increase in wetland habitat. Our findings highlight the importance of wetland habitat in predicting meningeal worm infection across eastern South Dakota. Future research is warranted to evaluate the relationships between climatic conditions (e.g., drought, wet cycles) and deer habitat selection in maintaining *P. tenuis* along the western boundary of the parasite.

*Key words:* Meningeal worm, *Odocoileus virginianus*, parasite, *Parelaphostrongylus tenuis*, South Dakota, wetland, white-tailed deer.

The meningeal worm (*Parelaphostrongylus tenuis*) is a nematode parasite that commonly infects white-tailed deer (*Odocoileus virginianus*; WTD) throughout deciduous forests of eastern and central North America (Lankester 2001; Wasel et al. 2003). The meningeal worm has an indirect life cycle requiring one of several species of terrestrial gastropods (Lankester and Anderson 1968). Consequently, spatial distribution of the parasite depends on climate and habitat factors that influence distribution of definitive (e.g., WTD) and intermediate (e.g., terrestrial gastropods) hosts and survival of first-stage larvae (Shostak and Samuel 1984; Lankester 2001). Previous studies have identified forest cover (Wasel et al. 2003; Maskey et al. 2015), spring temperature, and summer precipitation (Jacques et al. 2015) as important factors associated with prevalence of meningeal worm infection in deer (hereafter meningeal worm prevalence) in prairie-dominated habitats. Cool, wet microclimates in wooded habitats likely facilitate transmission of meningeal worms between intermediate and definitive host species (Lankester and Anderson 1968). Prevalence of infection across the Northern Great Plains (NGP) also may be influenced by availability of wetland habitats because moist microclimates likely minimize desiccation of first-stage larvae or help maintain a moist mucous coating on exterior surfaces of deer feces (Shostak and Samuel 1984). However, information on the relative importance of wetland habitats as potential meningeal worm transmission sites is conflicting (Jacques and Jenks 2003; Jacques et al. 2015; Maskey et al. 2015). Nevertheless, few studies have evaluated potential effects of forest and wetland habitats on meningeal worm prevalence within the grassland biome of central North America. We evaluated potential additive effects of habitat (i.e., percentage of wetland and forest cover) on climate variables (spring temperature [SPRT], summer precipitation [SUMP])

TABLE 1. Final variables and associated descriptive statistics used to model the influence of county-level habitat characteristics on meningeal worm (*Parelaphostrongylus tenuis*) prevalence in white-tailed deer (*Odocoileus virginianus*) in eastern South Dakota, USA, 1997–99.

| Variable name[a] | Description | $\bar{x}$ | SE |
|---|---|---|---|
| SPRT[b] | Mean 10-yr (1991–2000) spring temperature (C) | 6.34 | 0.66 |
| SUMP[b] | Mean 10-yr (1991–2000) summer precipitation (cm) | 9.00 | 0.86 |
| PLAND_FOR | Percentage of landscape in forested habitat | 0.77 | 0.63 |
| PLAND_WET | Percentage of landscape in wetland habitat | 3.74 | 2.44 |

[a] SPRT = spring temperature; SUMP = summer precipitation; PLAND_FOR = percent forested land; PLAND_WET = percent wetland.

[b] Calculated by Jacques et al. (2015) using climate data collected from 166 weather stations across South Dakota; these covariates comprised the best approximating model generated by Jacques et al. (2015) that was used as the base (constant) structure for all models.

identified by Jacques et al. (2015) as important predictors of meningeal worm prevalence across a region of eastern South Dakota characterized by relatively uniform climate and prevalence of infection with the parasite.

We used county-specific prevalence data collected by Jacques and Jenks (2004), and climate metrics (e.g., SPRT, SUMP; Table 1) collected by Jacques et al. (2015), to evaluate effects of climate and habitat characteristics (wetland and forested cover) on meningeal worm infection across eastern South Dakota (see Jacques et al. [2015] for a detailed description of the study area in eastern South Dakota). To reduce inaccurate prevalence estimates due to low sampling intensity, we limited our analyses to a subset of 27 counties east of the Missouri River where a minimum of 20 WTD were sampled (fig. 1 in Jacques et al. 2015). To estimate habitat characteristics, we clipped 2001 National Land Cover Data (Homer et al. 2007) from each county. We reclassified land cover data as forest, wetlands, or open water and used FRAGSTATS 4.2 (McGarigal et al. 2002) to calculate county-level habitat metrics (i.e., percent open water, percent forest, percent wetland). To minimize potential confounding effects of habitat metrics on predicting meningeal worm prevalence (i.e., larger counties have greater area of wetland or forested habitat), we limited our habitat model variables to percent forested land (PLAND_FOR) and percent wetland (PLAND_WET; Table 1). Because of the near linear relationship between percent open water and wetlands habitats, we excluded open water metrics from our analysis.

We used logistic regression to determine relationships between county-level habitat characteristics and probability of infection with *P. tenuis* in WTD populations across eastern South Dakota. Excluding the region covariate, we used the best approximating model generated by Jacques et al. (2015) as the base (constant) structure for all models constructed to account for maximum variation in prevalence data. Prior to modeling, we screened all predictor variables for collinearity ($|r|>0.5$; Jacques et al. 2015). We used four variables to determine effects of climate and habitat characteristics on probability of infection (Table 1). To test hypotheses about which of the habitat variables best explained meningeal worm prevalence, we constructed four candidate models by adding all possible combinations of uncorrelated habitat variables (i.e., PLAND_FOR, PLAND_WET) to the base model (SPRT+SUMP; Jacques et al. 2015). We used Akaike's information criterion corrected for small sample sizes ($AIC_c$) to select models that best described the data and used Akaike weights ($w_i$) as a measure of relative support (weight of evidence) for model fit; we considered models differing by $<2\ \Delta AIC_c$ from the best model as potential alternatives (Burnham and Anderson 2002).

Because of potential spatial autocorrelation in meningeal worm prevalence across eastern South Dakota, we evaluated the residuals of our best regression model by estimating the

TABLE 2. Akaike information criteria adjusted for small sample size ($AIC_c$) model selection of a priori logistic regression models for prevalence of meningeal worm (*Parelaphostrongylus tenuis*) in white-tailed deer (*Odocoileus virginianus*) in eastern South Dakota, USA, 1997–99.

| Model covariates[a] | K[b] | $AIC_c$ | $\Delta AIC_c$[c] | $w_i$[d] |
|---|---|---|---|---|
| PLAND_WET | 4 | 2,362.05 | 0.00 | 0.71 |
| PLAND_WET+ PLAND_FOR | 5 | 2,363.87 | 1.82 | 0.29 |
| PLAND_FOR | 4 | 2,376.87 | 14.82 | 0.00 |
| SPRT+SUMP[e] | 3 | 2,416.21 | 54.17 | 0.00 |

[a] PLAND_WET = percent wetland; PLAND_FOR = percent forested land; SPRT = spring temperature; SUMP = summer precipitation.

[b] No. of parameters.

[c] Difference in $AIC_c$ relative to minimum $AIC_c$.

[d] Akaike (model) weight or weight of evidence.

[e] Excluding region effects of the Missouri River, all models have the top model (SPRT+SUMP) from Jacques et al. (2015) as the base model to which we added habitat covariates.

overdispersion parameter ($\hat{c}$) and Moran's I statistic (Cliff and Ord 1981; Jacques et al. 2015); $\hat{c}$ should generally be $1 \leq \hat{c} \leq 4$, though in cases where $\hat{c}<1$, it is commonly recommended to use $\hat{c}=1$ (Burnham and Anderson 2002). We determined prediction capabilities of the best model with area under the receiver-operating-characteristic (ROC) curve; we considered ROC values between 0.5 and 0.7 to indicate low discrimination (Grzybowski and Younger 1997). We estimated potential effects of predictor variables on meningeal worm prevalence using odds ratios (OR; Freund and Wilson 2003). We conducted statistical analyses using SAS 9.2 (SAS Institute Inc. 2008).

The highest-ranked model for detecting probability of meningeal worm prevalence across eastern South Dakota was SPRT+SUMP+PLAND_WET (Table 2). Support for this model was substantial ($w_i$=0.71 and $\Delta$AIC>10), although predictive capability was low (ROC=0.62). In the second-ranked (global) model ($\Delta AIC_c$=1.82), 95% confidence intervals (CI) for parameter estimates of the PLAND_FOR covariate encompassed zero (0.061, SE=0.144, 95% CI= –0.221–0.343), indicating that it was not an important predictor of meningeal worm prevalence. All other models were noncompetive ($w_i$<0.001; Table 2); thus, we considered the highest-ranked model as the only model that fit the data. The logistic equation for the highest-ranked model was logit(μ; # positive deer/# deer tested by county) = –7.462+0.487(SPRT)+0.281(SUMP)+0.176 (PLAND_WET). The 95% CIs for parameter estimates of the SPRT (95% CI=0.313–0.661), SUMP (95% CI=0.168–0.395), and PLAND_WET (95% CI=0.130–0.223) covariates did not overlap zero, and *P*-values were significant ($P \leq 0.001$), indicating these variables were influential predictors of meningeal worm prevalence. Probability of meningeal worm prevalence increased by 1.33 (OR=1.325, 95% CI=1.183–1.484) per 1-cm increase in summer precipitation and by 1.63 (OR=1.628, 95% CI=1.368–1.936) per 1-C increase in spring temperature. In addition, probability of infection increased by 1.19 (OR=1.193, 95% CI=1.139–1.250) for each 1% increase in wetland habitat. Our estimate of $\hat{c}$ for the highest-ranked model (SPRT+SUMP+PLAND_WET) was 0.624. While Moran's I statistic was significant for the base model (SPRT+SUMP; $I$=0.002, $z$=12.840, $P$<0.001), there was no evidence of spatial autocorrelation in the best model ($I$ = –0.00008, $z$=1.67, $P$=0.094; Table 2). Thus, the PLAND_WET covariate accounted for spatial autocorrelation unaccounted for in the base model.

Strong associations between meningeal worm prevalence and wetland habitat across eastern South Dakota is not surprising given habitat preferences of WTD and the presumed role of wetland cover in moderating microclimate and, thus, terrestrial gastropod habitat (Naugle et al. 1997; Jacques and Jenks 2003). Positive associations between meningeal worm prevalence and availability of wetland cover across the NGP make biologic sense, given previously documented relationships among WTD movement patterns and wetland habitat selection across the Midwest. For example, Naugle et al. (1997) reported near-exclusive use of wetland habitats by WTD during years with normal water levels but substantially reduced use of wetlands during high water levels. Similar use of wetland habitats has been reported for WTD across southcentral Wisconsin (Larson et al. 1978).

Though population density of WTD across eastern South Dakota was unknown, it is possible that density was correlated with availability of wetland cover, which may be influenced by interannual variation in climatic factors. For example, the extent to which drought conditions influence availability of wetland habitats (and meningeal worm infection prevalence) across the NGP has not previously been evaluated. We hypothesize that during prolonged drought conditions throughout eastern South Dakota, odds of encounter between infected gastropods and WTD may increase due to greater spatial overlap around wetlands, which are characterized by cooler temperatures and reduced exposure to sunlight and which favors gastropods. Consequently, it is possible that wetland habitats may facilitate transmission of meningeal worms to local WTD during drought conditions and represent focal points for subsequent infection during postdrought years. Associations between meningeal worm prevalence, the distribution of wetland habitats in relation to climatic variation, and WTD habitat selection across grassland-dominated landscapes warrants further evaluation.

Contrary to Jacques et al. (2015), who found that spring temperature had little effect on meningeal worm infection across South Dakota, we found that spring temperature was positively related to prevalence. Perhaps important predictors (region, summer precipitation) identified by Jacques et al. (2015) masked the potential effects of spring temperature on meningeal worm prevalence found during our analysis. Our results partially support previous findings by Maskey et al. (2015), who noted positive associations between spring temperature, gastropod availability, percentage of woodland cover, and meningeal worm prevalence. However, forest habitat (e.g., shelterbelts) was not an important predictor of meningeal worm infection across eastern South Dakota. Many shelterbelts were comprised of linear tree plantings and grazed by domestic livestock, which may have produced unfavorable microclimates (e.g., reduced vegetation, low moisture) for terrestrial gastropods during our study.

Funding was provided by Federal Aid in Wildlife Restoration administered by South Dakota Department of Game, Fish and Parks, Study 7592, the Rocky Mountain Elk Foundation, and South Dakota State University. We appreciate the support provided by the Department of Natural Resource Management at South Dakota State University. We thank S. Meagher and two anonymous reviewers for providing helpful comments on earlier drafts of our manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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*Submitted for publication 2 February 2016.*
*Accepted 29 April 2016.*