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INFLUENCE OF ECOLOGIC FACTORS ON PREVALENCE OF MENINGEAL WORM (*PARELAPHOSTRONGYLUS TENUIS*) INFECTION IN SOUTH DAKOTA, USA

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ABSTRACT: The meningeal worm (*Parelaphostrongylus tenuis*) is a nematode parasite that commonly infects white-tailed deer (*Odocoileus virginianus*; WTD) throughout the deciduous forest biome and deciduous-coniferous ecotone of eastern and central North America; the species is not known to occur west of the grassland biome of central North America. We used county-specific prevalence data to evaluate potential effects of landscape and climatologic factors on the spatial distribution of meningeal worm infection in South Dakota, US. Probability of infection increased 4-fold between eastern and western South Dakota and 1.3-fold for each 1-cm increase in summer precipitation. Sixty-three percent of WTD had only a single worm in the cranium. Expansion of meningeal worm infection across western South Dakota may be inherently low due to the combined effects of arid climate and potential attributes of the Missouri River that limit regional movements by infected WTD. Use of landscape genetic analyses to identify potential relationships between landscape features and population genetic structure of infected deer and parasites may contribute to a greater understanding of regional heterogeneity in meningeal worm infection rates across South Dakota, particularly in counties adjacent to the Missouri River. Future research evaluating heterogeneity in prevalence and intensity of infection between fawn and yearling deer, and the potential role of yearling male deer as dispersal agents of meningeal worms across the Missouri River, also is warranted.

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

INTRODUCTION

The meningeal worm (*Parelaphostrongylus tenuis*) is a common and widely distributed parasite of white-tailed deer (*Odocoileus virginianus*; WTD) throughout eastern North America (Anderson 1972; Anderson and Prestwood 1981; Lankester 2001). Adult worms typically inhabit the subdural spaces of the brain, and first-stage larvae are excreted in mucus covering WTD feces (Anderson and Prestwood 1981). Completion of the life cycle requires suitable terrestrial gastropod (snails and slugs) intermediate hosts (Lankester and Anderson 1968; Lankester 2001). Wild ungulates become infected by ingesting infected gastropods while feeding (Anderson and Prestwood 1981). The parasite typically establishes benign infections in WTD, the definitive host, but can cause fatal neurologic disease in elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and caribou (*Rangifer tarandus*; Anderson 1971, 1972; Upshall et al. 1987; Lankester 2001; Larkin et al. 2003).

Meningeal worm infection has only been reported as far west as the Dakotas and western Nebraska in the USA (Oates et al. 2000; Jacques and Jenks 2004; Maskey and Vetter 2012) and eastern Saskatchewan in Canada (Wasel et al. 2003). Climatologic factors (e.g., precipitation, temperature) suspected of limiting transmission and spatial distribution of *P.*

tenuis likely influence the distribution of suitable gastropod intermediate hosts and survivability of first-stage larvae (Lankester and Anderson 1968; Anderson 1972; Kocan et al. 1982). In arid regions, repeated desiccation-rehydration cycles may reduce survival of first-stage *P. tenuis* larvae or contribute to periods of inactivity in terrestrial gastropods until the return of favorable conditions (Lankester and Anderson 1968).

Current hypotheses regarding spatial distribution of *P. tenuis* across central North America are conflicting. Previous work by Anderson (1972) and Samuel and Holmes (1974) suggested that the grassland biome of central North America acts as an ecologic barrier to the westward spread of the meningeal worm. Jacques and Jenks (2004) hypothesized that the Missouri River might be acting, in part, to limit the westward expansion of *P. tenuis* across South Dakota. In contrast, natural and artificial (e.g., irrigation of agricultural cropland) water sources may provide sufficient moisture to sustain adequate densities of gastropod intermediate hosts, facilitating the westward movement of *P. tenuis* across prairie-dominated habitats of northcentral North America (Oates et al. 2000; Wasel et al. 2003). To our knowledge, the only evaluation of landscape and climatic effects on prevalence and distribution of *P. tenuis* across northcentral North America was by Wasel et al. (2003), who suggested that low rainfall likely influenced the westernmost limit of *P. tenuis*. Moreover, Lankester (2010) noted a paucity of published data needed to test suspected relationships between climatologic and landscape factors and infection with *P. tenuis*.

Compared to other regions, landscapes across the northern Great Plains are characterized by short- and mixed-grass prairie habitat, agricultural cropland, limited forest cover, and an abundance of seasonal and temporary wetland basins (Euliss et al. 1999; Smith et al. 2002). Consequently, the ability to predict the influence of landscape and environmental variables on expansion of *P. tenuis* across the northern Great Plains could have important implications in the management of free-ranging ungulates, particularly elk and mule deer. Our objective was to quantify potential effects of landscape (e.g., wetland cover, grassland cover, acreage of irrigated farmland) and climatologic (e.g., temperature, precipitation) factors on the prevalence of infection with *P. tenuis* in WTD populations throughout South Dakota.

METHODS AND MATERIALS

We used county-specific prevalence data collected by Jacques and Jenks (2004) to evaluate the potential effects of landscape and climatologic factors on spatial distribution of meningeal worm infection in South Dakota. To maximize the likelihood of incorporating life-history factors influencing the gastropod intermediate hosts, we conducted our analyses using long-term (1991–2000) climatologic data (mean annual and seasonal temperature [C], mean annual and seasonal precipitation [cm], and number of precipitation days per year) collected from 166 weather stations across the state. Additionally, we quantified total hectares of agricultural farmlands (US Department of Agriculture [USDA] 2013) and total cover (%) of wetland and grassland habitats (South Dakota Gap Analysis Project; Smith et al. 2002) by county over 10 yr (1991–2000; Table 1) to evaluate potential effects of landscape and climatologic factors on the occurrence of *P. tenuis* across South Dakota. We used an information theoretic approach (Burnham and Anderson 2002) to evaluate potential associations among probability of infection (i.e., proportion of WTD infected) with *P. tenuis*, climate, and landscape factors by region (eastern vs. western South Dakota).

South Dakota is separated by the Missouri River into eastern and western regions (Fig. 1). Eastern and western South Dakota comprise 44 (35,356 km^2) and 22 (41,839 km^2) counties, respectively. Broadly speaking, landscape characteristics range from glaciated, gently rolling terrain with numerous pothole wetlands across eastern South Dakota to unglaciated rolling prairie interspersed with sagebrush (*Artemisia* spp.) throughout western South Dakota (Bryce et al. 1998). Eastern and western South Dakota are dominated by agriculture (50.4% of land use) and livestock

TABLE 1. Comparison of long-term (1991–2000) variation in landscape and climatologic factors in areas east and west of the Missouri River in South Dakota, USA. Asterisks denote regional differences ($P\leq0.05$) between variables. Units of measure for temperature and precipitation covariates are C and cm, respectively.

	West of river		East of river		
Variable[a]	Mean	SE	Mean	SE	*P*-value
AT*	7.836	0.219	7.131	0.213	0.041
SPRT	7.184	0.205	7.203	0.161	0.943
SUMT	21.445	0.291	20.428	0.469	0.981
FALLT	8.193	0.244	8.010	0.189	0.567
WINT*	−4.480	0.338	−7.120	0.259	<0.001
WET*	1.186	0.344	9.302	0.378	<0.001
IL*	53,371.609	14,129.100	26,253.791	3,756.203	0.020
GRASS*	67.459	3.505	36.527	1.806	<0.001
PD*	45.455	1.023	48.409	0.631	0.012
AP*	53.895	1.625	61.429	0.878	<0.001
SPRP	5.988	0.214	5.957	0.148	0.904
SUMP*	7.190	0.167	8.636	0.147	<0.001
FALLP*	3.514	0.207	4.582	0.074	<0.001
WINP	1.273	0.065	1.302	0.035	0.662

[a] AT = mean 10-yr annual temperature; SPRT = mean 10-yr spring (March–May) temperature; SUMT = mean 10-yr summer (June–August) temperature; FALLT = mean 10-yr fall (September–November) temperature; WINT = mean 10-yr winter (December–February) temperature; WET = total wetland cover (%); IL = 10-yr mean total hectares of irrigated land by county; GRASS = total grassland cover (%); PD = 10-yr mean number days ≥0.25 cm of precipitation per year; AP = mean 10-yr annual precipitation; SPRP = mean 10-yr spring precipitation; SUMP = mean 10-yr summer precipitation; FALLP = mean 10-yr fall precipitation; WINP = mean 10-yr winter precipitation.

grazing (70.8% of land use; Smith et al. 2002). Wetland habitat is limited throughout eastern (9.3%) and western (1.4%) South Dakota (Smith et al. 2002). South Dakota has a continental climate, averaging −6.9 C in winter and 21.3 C in summer. Mean annual precipitation and snowfall (1997–99) across eastern and western South Dakota was 52.0 cm and 80.9 cm, and 41.6 cm and 82.6 cm, respectively (South Dakota Office of Climatology 2009). Total area of irrigated farmland across eastern and western South Dakota (1987–2002) was 1,128,913 ha (SE=3,799) and 1,174,175 ha (SE=14,577), respectively (USDA 2013).

Data analyses

We used logistic regression to model potential ecologic effects on the probability of infection with *P. tenuis* in WTD populations across the state; thus, precision of our response variable was directly related to the number of WTD sampled and potential landscape (e.g., total wetland cover [WET], total acreage of irrigated farmland by county [IL], total grassland cover [GRASS], region [eastern vs. western South Dakota; REG]) and climatologic (e.g., annual temperature [AT], annual precipitation [AP], spring (March–May) temperature [SPRT], spring precipitation [SPRP], summer (June–August) temperature [SUMT], summer precipitation [SUMP], fall (September–November) temperature [FALLT], fall precipitation [FALLP], winter (December–February) temperature [WINT], winter precipitation [WINP], and number of precipitation days [PD]) effects by county. We used Akaike's Information Criterion (AIC) to select models that best described the data and used Akaike weights (w_i) as a measure of relative support for model fit (Burnham and Anderson 2002).

Because of strong potential spatial relatedness in the meningeal worm-WTD infection system, we evaluated whether spatial autocorrelation was present in the residuals (i.e., measure of deviance contributed from each observation) of our optimal regression model by estimating the overdispersion parameter, $\hat{c}$. We calculated $\hat{c}$ by dividing the deviance statistic by the associated degrees of freedom for the optimal model (Venables and Ripley 2002). The estimated overdispersion parameter should generally be $1\leq\hat{c}\leq4$ (Burnham and Anderson 2002), though it is commonly recommended to correct for any $\hat{c}>1$ (G. C. White pers. comm.). To account for overdispersion in our data, we adjusted the variance-covariance matrix using our estimate of $\hat{c}$. We computed and subsequently used Quasi-AIC estimators for model selection and

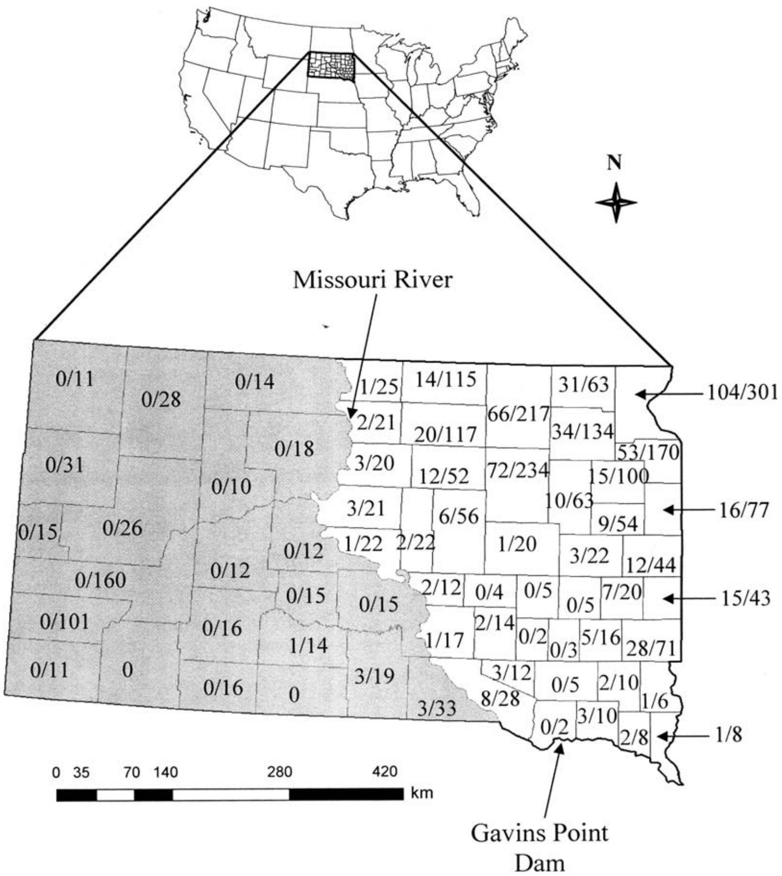

FIGURE 1. Meningeal worm (*Parelaphostrongylus tenuis*) study areas were located in eastern and western (shaded gray) South Dakota, USA, 1997–99. Note separation of eastern from western South Dakota by the Missouri River. Thick (external) black lines delineate the state boundary. Thin (internal) black lines delineate county boundaries (n=66). Numbers within county boundaries denote prevalence (number of white-tailed deer [*Odocoileus virginianus*] infected/total number sampled) of meningeal worm infection across eastern and western South Dakota. Note the location of Gavins Point Dam (GPD) along the Nebraska border, above which the Missouri River is characterized by large, man-made impoundments with expansive, lake-like conditions. Below GPD, the River is more representative of riverine conditions and is narrower than the impoundments upstream of the dam.

readjusted the number of model parameters to account for the estimation of $\hat{c}$ (Burnham and Anderson 2002). Additionally, we determined predictive capabilities of models with area under the receiver operating characteristic (ROC) curve; we considered ROC values between 0.5 and 0.7 low discrimination, values between 0.7 and 0.8 acceptable discrimination, and values ≥0.8 excellent discrimination (Grzybowski and Younger 1997; Hosmer and Lemeshow 2000). We determined associations between response and predictor variables using odds ratios (OR); OR for predictor variables are the relative amount by which the odds of the outcome increase (OR>1.0) or decrease (OR<1.0) with each unit increase in the predictor variable (Freund and Wilson 2003).

We used simple *t*-tests to determine differences in landscape and climatic factors between eastern and western South Dakota. We used Pearson's chi-square (χ^2) analyses and one-factor analysis of variance to test for differences in intensity of meningeal worm infection by region and between deer age and sex classes. We defined adult deer as ≥18 mo at harvest, yearlings as 6–18 mo at harvest, and fawns as <6 mo at harvest (Jacques et al. 2009). We conducted statistical analyses using SYSTAT (SYSTAT Software Inc., Richmond, California; Wilkinson 1990). We set alpha at ≤0.05 and we used Bonferonni correction factors to maintain experiment-wide error rates when performing multiple χ^2 analyses and *t*-tests (Neu et al. 1974).

RESULTS

We documented no difference ($t_{64}\leq$ 0.439, $P\geq0.567$) in mean (1991–2000) spring temperature, summer temperature, fall temperature, spring precipitation, or winter precipitation between eastern and western South Dakota, where prevalence of *P. tenuis* was 25.3% (n=2,271 WTD) and 1.2% (n=577 WTD), respectively (Table 1; Jacques and Jenks 2004). In contrast, annual temperature, winter temperature, percent grassland, and total acreage of irrigated land were lower ($t_{64}\geq-7.109$, $P\leq0.041$) in eastern than in western South Dakota. Further, percent wetland, number of precipitation days, annual precipitation, summer precipitation, and fall precipitation were higher ($t_{64}\geq2.575$, $P\leq0.012$) in eastern than in western South Dakota (Table 1). Infected WTD were collected from 37 of 44 counties and three of 22 counties in eastern and western South Dakota, respectively (Jacques and Jenks 2004; Fig. 1).

We recorded the number of meningeal worms in 472 of 578 infected WTD. Mean intensity of infection was 1.63 (SE=0.05) worms per cranium, though it ranged from 0 to 11 worms per cranium. One worm was recovered from 63% (n=296) of infected WTD, whereas 2 and ≥3 worms were recovered from 24% (n=113) and 13% (n=63), respectively, of craniums examined for the parasite. Intensity of infection was higher ($F_{2,469}=7.34$, $P=0.001$) in adult deer ($\bar{X}=1.60$, SE=0.24, n=257) than in fawn ($\bar{X}=1.34$, SE=0.14, n=77) age classes. Additionally, intensity of infection was higher ($F_{1,470}=6.32$, $P=0.012$) in females ($\bar{X}=1.70$, SE=0.06, n=396) than in male deer ($\bar{X}=1.33$, SE=0.14, n=76).

A priori models predicting probability of meningeal worm infection

The highest-ranked model for detecting probability of meningeal worm infection across South Dakota was REG+SPRT +SUMP (Table 2). Support for this model was substantial ($w_i=0.993$), though predictive capability was low (ROC=0.661; Table 2); all other models were noncompetitive ($w_i<0.007$; Table 2). The logistic equation for this model was $\text{logit}(\mu)=-5.703+1.394\,(\text{REG})+0.102\,(\text{SPRT})+0.282\,(\text{SUMP})$. In the highest-ranked model, 95% confidence intervals (CI) for parameter estimates of the REG (95% CI=0.815–1.597) and SUMP (95% CI=0.236–0.463) covariates did not overlap zero and *P*-values were significant ($P\leq0.0001$), indicating that these variables were influential predictors of meningeal worm infection. However, 95% confidence intervals for parameter estimates of the SPRT covariate (95% CI=0.256–0.072) overlapped zero and the *P*-value was not significant ($P=0.103$), suggesting that this variable had little effect on meningeal worm infection across South Dakota. Our estimate of $\hat{c}$ for the highest-ranked model was 2.603.

Probability of meningeal worm infection increased 4.03 (OR=4.032, 95% CI=2.732–5.951) between eastern and western South Dakota. Similarly, probability of infection increased by 1.33 (OR=1.326, 95% CI=1.185–1.484) for each 1-cm increase in summer precipitation. Although not statistically significant, probability of infection increased by 1.11 (OR=1.107, 95% CI=0.980–1.252) for each 1 C increase in mean spring temperature.

DISCUSSION

Prevalence of meningeal worm infection in South Dakota was best described by a model containing geographic region and mean summer precipitation. Our findings make biologic sense and confirm previous hypotheses regarding factors limiting the westernmost distribution of *P. tenuis* in the grassland biome of the northern Great Plains, most notably that the Missouri River likely acts as a physical barrier to reduce movement of *P. tenuis* into western South Dakota (Jacques and Jenks 2004).

TABLE 2. Akaike's Information Criteria (AIC) model selection of a priori logistic regression models for meningeal worm distribution in South Dakota, USA, 1997–99. Units of measure for temperature and precipitation covariates were C and cm, respectively.

Model covariates[a]	K[b]	QAIC[c]	ΔQAIC[d]	w_i[e]
REG+SPRT+SUMP	5	994.489	0.000	0.993
REG+SPRP	4	1,004.721	10.232	0.006
REG	3	1,008.043	13.554	0.001
GRASS+SUMT+FALLP	5	1,012.021	17.532	0.000
GRASS	3	1,023.914	29.425	0.000
SUMT+SUMP	4	1,032.252	37.763	0.000
FALLT+FALLP+PD+AP	6	1,027.197	32.708	0.000
AP+AT	4	1,040.259	45.770	0.000
WET+SPRP+SUMT	5	1,040.365	45.876	0.000
WET+SPRP	4	1,045.173	50.684	0.000
WET	3	1,048.384	53.895	0.000
IL+SPRP+SUMT	5	1,066.100	71.611	0.000
IL	3	1,078.438	83.949	0.000
PD	3	1,086.017	91.528	0.000

[a] REG = Eastern vs. western South Dakota; SPRT = mean 10-yr spring (March–May) temperature; SUMP = mean 10-yr summer precipitation; GRASS = total grassland cover (%); SUMT = mean 10-yr summer (June–August) temperature; FALLP = mean 10-yr fall precipitation; WET = total wetland cover (%); SPRP = mean 10-yr spring precipitation; AP = mean 10-yr annual precipitation; AT = mean 10-yr annual temperature; FALLT = mean 10-yr fall (September–November) temperature; PD = 10-yr mean number days ≥0.25 cm of precipitation per year; IL = 10-yr mean total acreage (ha) of irrigated land by county.

[b] Number of parameters.

[c] Quasi-AIC (QAIC) adjusted for overdispersed data.

[d] Difference in Quasi-AIC (QAIC) relative to minimum QAIC.

[e] Akaike (model) weight.

Using intensive statewide sampling, Jacques and Jenks (2004) reported that meningeal worm infection was limited to a region west of the Missouri River (Fig. 1) along the Nebraska border. It remains uncertain whether the source of infected WTD in western South Dakota originated in the eastern region of the state or was associated with immigration of animals from Nebraska. Nevertheless, the association between limited distribution of meningeal worm infection across western South Dakota and presumed movements of WTD across the Missouri River suggests that potential crossing sites occur primarily along the Nebraska border (e.g., Gavin's Point Dam; Fig. 1), despite evidence in contrast to these movements. For instance, Haffley (2013) noted no movement of radio-collared deer across the Missouri River from South Dakota into Nebraska, and Jacques and Jenks (2003a) reported the only documented case of an infected mule deer that died just north of the Nebraska border in Charles Mix County, South Dakota. Though our findings support the Missouri River barrier hypothesis previously postulated by Jacques and Jenks (2004), further evaluation of the physical attributes of the river (e.g., width, water velocity, water flow, dam construction, channelization) and regional WTD movement patterns are needed to facilitate increased understanding of the meningeal worm-WTD infection system across the grassland biome of northcentral North America. Use of landscape genetic analyses to identify potential relationships between landscape features and population genetic structure of infected deer (Blanchong et al. 2008) and parasites may contribute to a greater understanding of regional heterogeneity in meningeal worm infection rates across South Dakota, particularly in counties adjacent to the Missouri River. Further evaluation of ecologic factors over multiple years and that vary temporally (e.g., by year) also may aid in a better understanding of the meningeal worm-WTD infection system across the northern Great Plains region.

A strong association between spatial distribution of meningeal worm infection and seasonal precipitation is not surprising given regional heterogeneity in climatologic factors across South Dakota and the interrelationships between *P. tenuis* and suitable intermediate hosts (Lankester and Anderson 1968; Shostak and Samuel 1984; Jacques and Jenks 2003b). Counties east of the Missouri River were characterized by higher ($P<0.001$) precipitation (annual, summer, and fall) and greater ($P<0.001$) number of precipitation days per year than counties west of the Missouri River. Establishment of the parasite in the tri-county region of western South Dakota (Jacques and Jenks 2003b) raises concern that future range expansion of the parasite into additional counties west of the Missouri River, including the Black Hills region, is possible. However, low rainfall likely influences the westernmost limit of meningeal worms across the central grassland biome and, thus, limits the potential for transmission of the parasite to vulnerable cervid populations across northcentral North America (Wasel et al. 2003).

Our results indicate that western South Dakota provides unfavorable conditions (low precipitation, high ambient temperatures) for expansion of the range of meningeal worms to additional counties throughout the rangelands west of the Missouri River. Of equal importance is the high proportion (63%) of infected WTD throughout eastern South Dakota that had only one worm in the cranium, which is an expected consequence of low transmission rates (Lankester 2010). Slomke et al. (1995) hypothesized that large proportions of WTD infected with only one worm are immunized and thought never to develop patent infections. Our findings also indicate low infection rates in adult female deer as well as in traditionally dispersing sex (male) and age (yearling) classes. Thus, likelihood of expansion of the range of meningeal worms across western South Dakota may be inherently low due to the combined effects of arid climatic conditions, low parasite transmission rates (particularly among dispersing animals), and potential effects of the Missouri River that limit regional movements by infected WTD. However, evaluating interrelationships among spatial distributions and densities of WTD and intermediate hosts along reaches of the Missouri River (e.g., southeastern South Dakota) that could potentially facilitate movement of *P. tenuis* from infected to uninfected regions of the state is warranted. Of particular interest would be future research evaluating heterogeneity in prevalence and intensity of infection between fawn and yearling deer age classes and the potential role of yearling male deer as dispersal agents of meningeal worms across the Missouri River. Our findings are important because, to our knowledge, few studies have presented empirical data quantifying the relative magnitude of potential ecologic effects limiting the spatial distribution of *P. tenuis* across the grassland biome of northcentral North America.

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