MENINGEAL WORM (PARELAPHOSTRONGYLUS TENUIS) IN SOUTH DAKOTA: THE PARASITE IN TERRESTRIAL GASTROPODS

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ABSTRACT

Terrestrial gastropods were collected from wetland, grassland, and forested habitats throughout eastern and southcentral South Dakota from May-August of 1999 and 2000 to assess the role of gastropods in transmission of meningeal worm (Parelaphostrongylus tenuis) to white-tailed deer (Odocoileus virginianus) populations throughout the state. A total of 4,063 gastropods representing 14 species, five of which were known intermediate hosts for P. tenuis, were collected throughout South Dakota during the summers of 1999 and 2000. Significantly more (P < 0.0001) gastropods were collected from eastern than western South Dakota. Six species of snails (Zonitoides nitidus, Z. arboreus, Discus cronkhitei, Succinea ovalis, Gastrocopta pentadon, and Vallonia sp.) and one slug species (Deroceras laeve) accounted for 87% of the gastropods collected. A total of 3,468 gastropods were examined for presence of P. tenuis larvae. Three species of snails (Z. arboreus, Z. nitidus, and D. cronkhitei) and one slug species (Deroceras laeve) accounted for 93% of the total number of infected gastropods (i.e., 66 of 71). Significantly more (P = 0.005) infected gastropods were collected from semipermanent wetlands than from grasslands or forested habitats, suggesting that wetland habitats are important transmission sites of P. tenuis from gastropods to white-tailed deer in South Dakota.

Keywords
Gastropod, intermediate host, meningeal worm, Parelaphostrongylus tenuis, prevalence, South Dakota, white-tailed deer

INTRODUCTION

Meningeal worm (Parelaphostrongylus tenuis) is a nematode parasite that infects white-tailed deer (Odocoileus virginianus) populations throughout eastern North America (Eckroade et al. 1970, Carpenter et al. 1972, Thurston and Strout 1978). Although P. tenuis typically does not cause neurologic disease in white-tailed deer, its usual host, natural infection in moose (Alces Alces) (Smith and Archibald 1964, Anderson 1965), elk (Cervus elaphus nelsoni) (Anderson...
et al. 1966, Carpenter et al. 1973), fallow deer (*Dama dama*) (Kistner et al. 1977, Davidson et al. 1985), caribou (*Rangifer tarandus*) (Trainer 1973), and reindeer (*Rangifer tarandus tarandus*) (Anderson 1971) typically resulted in severe neurologic disease. Experimental infection in mule deer (*O. hemionus*) (Tyler and Hibler 1980) and black-tailed deer (*O. h. columbianus*) (Nettles and Prestwood 1977) also resulted in severe neurologic disease.

Distribution of *P. tenuis* infected white-tailed deer also is dependent on the presence of suitable terrestrial gastropod intermediate hosts (Gleich et al. 1977, Maze and Johnstone 1986, Upshall et al. 1986). Although many species of terrestrial snails and slugs act as suitable *P. tenuis* intermediate hosts, several species are the most abundant and most commonly infected. Gleich and Gilbert (1976) documented two snail species (*Discus cronkhitei*, *Zonitoides arboreus*) and two slug species (*Deroceras reticulatum*, *D. laeve*) to be the most abundant and most commonly infected species in central Maine. Van Es and Boag (1981) also found *Z. arboreus* and *D. cronkhitei* to be important in transmission of the parasite in central Alberta. Upshall et al. (1986) found that *D. laeve* accounted for 40% of the gastropods collected in New Brunswick. Although Wasel (1995) documented 14 species of terrestrial gastropods, six of which were known *P. tenuis* intermediate hosts in eastern North Dakota, no attempt was made to determine the number of individuals infected with meningeal worm. To our knowledge, the role of terrestrial gastropods in transmission of *P. tenuis* to white-tailed deer populations in South Dakota has not been documented. The objectives of this study were to determine distribution and relative abundance of terrestrial gastropods populations throughout South Dakota, to determine which species of gastropods are most important in transmission of *P. tenuis* to white-tailed deer populations in South Dakota, and to determine the number of *P. tenuis* infected gastropods with respect to habitat type and time of year in South Dakota.

**STUDY AREA**

As a whole, South Dakota is characterized by prairie grassland and is composed of two regions (e.g., eastern and western South Dakota), which are separated by the Missouri River (Fig. 1). Eastern South Dakota is comprised of the Prairie Coteau, Missouri Coteau, and James River Lowland Physiographic Regions (Westin et al. 1967). Brookings, Beadle, and Hughes counties (Fig. 1) are representative counties of the Prairie Coteau, James River Lowland, and the Missouri Coteau physiographic regions, respectively. Eastern South Dakota is characterized as mid- and tall grass prairie habitat (Higgins 1999) and contains more water and receives more precipitation than semi-arid areas of western South Dakota (Johnson 1995).

Western South Dakota (Fig. 1) is comprised of the Pierre Hills, Northern Plateau, Southern Plateau, and Black Hills physiographic regions. Most of the area in western South Dakota is treeless, semi-arid, rolling upland characterized as mixed grass prairie habitat (Johnson 1976, Johnson 1988) that is drier and receives less precipitation than areas of eastern South Dakota. Gregory,
Tripp, and Lyman counties (Fig. 1) lie in the Great Plains and Southern Plateau physiographic regions of western South Dakota.

**MATERIALS AND METHODS**

Terrestrial gastropods were collected from the wet meadow zone of semi-permanent wetlands, mid-grass prairie habitats, and forested habitats in Brookings, Beadle, and Buffalo counties from May-August 1999 and in Gregory, Mellette, and Lyman counties from May-August 2000. Gastropods were collected from five randomly selected study locations per habitat type per county sampled. Gastropods were trapped using 30 x 30 cm cardboard traps (Gleich and Gilbert 1976). Traps were soaked in water and laid flat on the ground. In each study location, a location center was chosen. Once the location center was chosen, a random compass bearing was taken and traps were placed every 15 m along a 150-m transect. All traps were consecutively numbered along established transect lines. There were four gastropod collection periods (15-30 May, 15-30 June, 15-30 July, 15-30 August) and collection in each of the six counties was completed in one to two days. Following each collection period, each trap was soaked in water and randomly relocated three meters from the original trap location.
Gastropods were identified according to the criteria of Pilsbry (1940, 1946, 1948). To detect the presence of *P. tenuis* larvae recovered from collected gastropods, gastropods were artificially digested using a pepsin-HCl procedure described by Kocan (1985). Gastropod tissue placed in petri dishes was artificially digested in a solution of 1.0% pepsin and 1.0% HCl for four to six hours at 37° C. Slides prepared with all of the digestate were examined microscopically for meningeal worm larvae. Infective third-stage *P. tenuis* larvae were distinguished from other nematode larvae based on body measurements and tail morphology (Anderson 1963, Ballantyne and Samuel 1984).

**RESULTS**

A total of 4,063 terrestrial gastropods representing 14 species, five of which were known intermediate hosts for *P. tenuis*, were collected throughout South Dakota during the summers of 1999 and 2000. Six species of snails (*Z. nitidus, Z. arboreus, D. cronkhitei, Succinea ovalis, Gastrocopta pentadon*, and *Vallo- nia* sp.) and one slug species (*Deroceras laeve*) accounted for 87% of the gastropods collected (Table 1). *Deroceras laeve* was the most ubiquitous species and was collected from each of the three habitat types in all six counties. Furthermore, 36 of 71 (51%) infected gastropods were *D. laeve*. Three species of snails (*Z. arboreus, Z. nitidus, and D. cronkhitei*) accounted for 42% of the total number of infected gastropods. Furthermore, *S. ovalis* also was found to be infected with *P. tenuis* (Table 1).

<table>
<thead>
<tr>
<th>Gastropod species</th>
<th>Number collected</th>
<th>Known intermediate hosts¹</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Snails</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Zonitoides arboreus</em></td>
<td>229</td>
<td>*</td>
</tr>
<tr>
<td><em>Gastrocopta pentadon</em></td>
<td>832</td>
<td></td>
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<tr>
<td><em>Euconulus fulvus</em></td>
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<td><em>Helicodiscus parallelus</em></td>
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<tr>
<td><em>Vallonia</em> sp.</td>
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<td></td>
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<td><em>Hawaii</em> minuscula</td>
<td>205</td>
<td></td>
</tr>
<tr>
<td><em>Succinea ovalis</em></td>
<td>472</td>
<td>*</td>
</tr>
<tr>
<td><em>Succinea avara</em></td>
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</tr>
<tr>
<td><em>Zonitoides nitidus</em></td>
<td>342</td>
<td>*</td>
</tr>
<tr>
<td><em>Discus cronkhitei</em></td>
<td>489</td>
<td>*</td>
</tr>
<tr>
<td><em>Oxyloma</em> sp.</td>
<td>55</td>
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<tr>
<td><em>Vertigo</em> sp.</td>
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<tr>
<td><em>Haplotrema</em> sp.</td>
<td>16</td>
<td></td>
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<tr>
<td><strong>Slugs</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Deroceras laeve</em></td>
<td>774</td>
<td>*</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>4,063</strong></td>
<td></td>
</tr>
</tbody>
</table>

¹ Known intermediate hosts in the literature and this study.
Relative abundance of gastropods was significantly higher ($\chi^2 = 280.72$; $df = 28, 3561; P < 0.0001$) in eastern ($n = 3,221$) than in western South Dakota ($n = 841$). There were no significant differences ($F = 1.40; df = 2, 3464; P = 0.246$) in relative abundance of gastropods between semipermanent wetlands ($n = 1,320$), forested habitats ($n = 1,750$), or grassland habitat types ($n = 993$) throughout eastern and western South Dakota.

A total of 3,468 randomly selected gastropods were examined for the presence of $P. tenuis$ larvae. Prevalence of infection with $P. tenuis$ in gastropods differed significantly ($F = 5.33; df = 2, 3467; P = 0.005$) between habitat types. Significantly more infected gastropods were collected from semipermanent wetlands (mean = 0.033, SE = 0.004) than from grasslands (mean = 0.016, SE = 0.005) or forested habitats (mean = 0.015, SE = 0.004). There was no significant difference ($F = 0.094; df = 1, 2457; P = 0.759$) in prevalence of infection between grassland and forested habitat types. Prevalence of infection did not differ with time of year ($F = 2.476; df = 3, 3466; P = 0.060$). Similarly, 33 of 71 (46.5%) infected gastropods were collected from semipermanent wetlands while 23 of 71 (32.4%) infected gastropods were collected from forested habitats. Only 15 of 71 (21%) infected gastropods were collected in mixed-grass prairie habitats. Furthermore, 72% (51/71) of infected gastropods were collected in June (24 of 71 infected gastropods) and July (27 of 71 infected gastropods). Only eight of 71 (11.3%) infected gastropods were collected in May. And 12 of 71 (16.9%) infected gastropods were collected in August.

**DISCUSSION**

For $P. tenuis$ to become established in a region, a number of ecological conditions must first be satisfied to facilitate transmission, including the presence of suitable terrestrial gastropod intermediate hosts. In this study, significantly ($P < 0.0001$) more gastropods were collected in eastern than in western South Dakota. This may be related to differences in precipitation and wetland density between the two regions of the state. Johnson (1995) reported a higher prevalence of wetland habitats in eastern than in western South Dakota. Furthermore, eastern South Dakota receives more rain than drier areas of western South Dakota (Johnson 1995). Upshall et al. (1986) suggested that gastropods prefer habitats that provide a moist refuge in which to estivate during hot, dry weather. Eastern South Dakota may provide more suitable gastropod habitat than western South Dakota.

Similarities in gastropod abundance between habitat types in South Dakota possibly reflects the difficulty in obtaining an accurate numerical assessment of gastropod abundance due to the influence of temperature change and variable precipitation throughout the trapping period (May-August). Boag (1990) reported that gastropod population estimates are confounded by the high variance in the number of gastropods collected at any one trapping period. In this study, abundance of gastropods varied unpredictably with daily temperature, precipitation, time of day during gastropod collections, and trap condition...
(e.g., wet vs. dry) upon recovery of gastropods. In a study to assess the validity of gastropod abundance estimates using cardboard traps, Wasel (1995) found that repeated surveys of the same area revealed that species richness was most consistent when traps remained damp, undisturbed, and checked during cooler daytime temperatures associated with early morning. The time of day gastropods were recovered and the frequent dry condition of the traps at the time of recovery possibly contributed to the lack of a significant difference in gastropod relative abundance between habitat types in South Dakota. Furthermore, collection activities often extended into mid-afternoon when daily temperatures were at or approaching a maximum. In these hot, dry conditions it is unlikely that gastropods sought refuge under traps.

Prevalence of infection with *P. tenuis* was significantly (*P* = 0.005) higher in gastropods collected from wetland habitats than from forested or mixed-grass prairie habitats. Upshall et al. (1986) suggested that hardwood forests in New Brunswick may have served as important *P. tenuis* transmission sites from infected gastropods to deer and moose due to the availability of gastropods and the feeding site selection of these ungulates. Stewart and Kandrud (1971) reported that the wet meadow zone of semipermanent wetlands in the glaciated prairie region were mostly dominated by low to medium-height grasses, rushes, sedges, and forbs or woody vegetation. Moreover, white-tailed deer have been described as concentrate selectors, meaning they selectively forage for high-quality, easily digestible plant parts (Demarais et al. 2000). Regular sampling from a wide range of species allows deer to continually evaluate new sources of nutrition (Demarais et al. 2000). Vegetation consumed in the wet meadow zone of semipermanent wetlands may provide deer with a high-quality, easily digestible energy source. Furthermore, 46.5% (33/71) of infected gastropods were collected from the wet meadow zone of semipermanent wetlands, we suggest that wetland habitats are important transmission sites of *P. tenuis* from gastropods to white-tailed deer in South Dakota.

Prevalence of infection with *P. tenuis* in gastropods did not differ (*P* = 0.060) with time of year, however, differences tended toward significance. In this study, 72% (51/71) of infected gastropods were collected between 5 June and 31 July. Only eight of 71 (11.3%) infected gastropods were collected in May while 12 of 71 (16.9%) infected gastropods were collected in August. Upshall et al. (1986) suggested the low number of gastropods infected in May would be an important factor with respect to potential transmission of infected gastropods to cervids. Getz (1959) reported that *D. laeve* is seldom active at temperatures below 14° C and was relatively unavailable for ingestion by deer and moose until this temperature was reached. In South Dakota, it is possible that cooler spring temperatures might restrict gastropod activities, rendering them relatively unavailable for ingestion by foraging white-tailed deer until a minimum ambient temperature is reached. We suggest that most white-tailed deer in South Dakota likely become infected with *P. tenuis* between mid-June and late July.

Upshall et al. (1986) and Lankester and Anderson (1968) found *D. laeve* to be the most abundant and most commonly infected intermediate host in New Brunswick and Navy Island, Ontario, respectively. Furthermore, Lankester and
Anderson (1968) reported that relative to other gastropod species collected, *D. laeve* was unusually active on Navy Island. In this study, *D. laeve* was the most abundant and most heavily infected gastropod collected in South Dakota. Because *D. laeve* has been reported as being unusually active, it is likely that these individuals encountered greater numbers of infective third stage *P. tenuis* larvae than other known intermediate host species. The importance of *D. laeve* as an intermediate host in South Dakota might possibly reflect the activity level of this species.

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LITERATURE CITED


