DIVERSITY AND ABUNDANCE OF TERRESTRIAL GASTROPODS IN VOYAGEURS NATIONAL PARK, MN: IMPLICATIONS FOR THE RISK OF MOOSE BECOMING INFECTED WITH *PARELAPHOSTRONGYLUS TENUIS*

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ABSTRACT: Voyageurs National Park (VNP) has a stable population of about 40–50 moose (*Alces alces*). Recent declines in moose abundance in adjacent areas in northern Minnesota raise concerns about the long-term viability of moose in VNP. The parasitic nematode *Parelaphostrongylus tenuis* has been documented in moose in VNP and has been implicated in moose declines in other populations. Terrestrial gastropods are the intermediate hosts for *P. tenuis*, and describing spatial and temporal differences in their abundance should increase understanding about the risk of *P. tenuis* infection for VNP moose at the individual and population levels. We used cardboard sheets to estimate species composition and abundance of terrestrial gastropods in representative vegetation communities in VNP. We collected a total of 6,595 gastropods representing 25 species, 22 terrestrial snails and 3 slugs; 8 are known vectors of *P. tenuis*, including the slug *Deroceras laeve*, the most common species found. Gastropods were more abundant in September than July, and in upland forests (maximum = 555 gastropods/m^2) more than in wetter lowlands (20 gastropods/m^2). We used location data from GPS-collared moose in VNP to estimate the relative exposure of moose to gastropods that could be infected with *P. tenuis* larvae. The boreal hardwood forest and northern spruce-fir forest ecotypes had the highest use by moose and high abundance of *P. tenuis* vectors in summer, and may pose the greatest risk for infection. Habitat use and the related risk of ingesting gastropod vectors varied by individual moose. Our method can be extended in moose range to estimate the relative risk of *P. tenuis* infection.

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Key Words: *Alces*, meningeal worm, Minnesota, moose, *P. tenuis*, parasite

INTRODUCTION

The parasitic nematode *Parelaphostrongylus tenuis* can be fatal to moose (*Alces alces)* (Anderson 1964), and was the probable cause of 5% of mortality of radio-collared moose in northwestern Minnesota and >20% of incidentally-recovered moose in northern Minnesota (Murray et al. 2006, Wünschmann et al. 2014). The infection causes weakness in the hindquarters, circling, tilting of the head, and increased fearlessness of humans (Anderson and Prestwood 1981). Infections can be lethal and cause mortality indirectly through increased risk of predation or accidents (Lankester et al. 2007, Butler et al. 2009, Wünschmann et al. 2014). Voyageurs National Park (VNP) in northern Minnesota maintains a stable, low-density population of about 40–50 moose, and *P. tenuis* infection and associated mortality has been documented in and surrounding VNP (Windels 2014). Though the effect on moose at the population level in VNP is unknown, previous studies suggest it is unlikely to be a major mortality source at the currently low white-tailed deer (*Odocoileus virginianus*) density (3–6 deer/km^2) (Whitlaw and Lankester 1994b).

The normal lifecycle of *P. tenuis* includes white-tailed deer as the definitive host and terrestrial gastropods as intermediate hosts (Lankester and Anderson 1968). White-tailed deer ingest infected gastropods while foraging and gastropods become infected with *P. tenuis* by crawling over or near infected deer feces (Lankester 2001). However, only 0.1–4.2% of gastropods collected in Minnesota and Ontario were infected with *P. tenuis* larvae (Lankester and Anderson 1968, Lankester and Peterson 1996). At those infection rates, a white-tailed deer would need to consume up to 1000 gastropods to encounter a single larva (Lenarz 2009). However, Lankester and Peterson (1996) reasoned that even at such low rates of infection in gastropods, the high rates of infection measured in white-tailed deer in the region (≤91%, Slomke et al. 1995) is explained by the large volume of vegetation eaten on and near the ground over a few months in the autumn. Infection rates in white-tailed deer derived from winter fecal samples have ranged from 67–90% from the 1970s to the present in VNP (Gogan et al. 1997, VanderWaal et al. 2014). White-tailed deer are the definitive host of *P. tenuis* but moose, an aberrant host, also ingest infected gastropods during foraging and become infected. Initial signs of *P. tenuis* infection can appear in moose as early as 20 days after experimental infection (Lankester 2002).

Gastropods are necessary for *P. tenuis* to complete its life cycle. Therefore, knowledge of gastropod populations in VNP may help managers better understand the role of *P. tenuis* in local moose population dynamics. The distribution and habitat preferences of terrestrial gastropods in VNP have not been studied previously. Extrapolation from studies of gastropod communities in different regions of Minnesota and the surrounding areas is possible (e.g., from northwestern Minnesota [Nekola et al. 1999] or rock outcrops in northeastern Minnesota [Nekola 2002]). Gastropods exhibit habitat preferences that result in variation in presence or density across vegetation communities or other habitat features, and few studies have examined their abundance and diversity at fine spatial scales (Moss and Hermanutz 2010).

The risk of *P. tenuis* infection is presumably influenced by vector density and could vary within a population because individual moose demonstrate differential habitat use (Gillingham and Parker 2008). Fine-scale habitat use derived from GPS collars can help clarify the risk of *P. tenuis* infection to individuals and populations of moose. Combined, individual differences in habitat use and variability among habitat types in gastropod diversity and abundance may result in differential risk of moose and other cervids to *P. tenuis* infection (VanderWaal et al. 2014).

In this study we surveyed terrestrial gastropod species on the Kabetogama Peninsula in VNP. Our objectives were to 1) estimate the abundance and diversity of terrestrial gastropods in different ecotypes, with particular focus on known vectors of *P. tenuis,* 2) document changes in gastropod abundance over the growing season, and 3) compare the use of cover types by GPS-collared moose to density of *P. tenuis* vectors to estimate the encounter risk of individual moose.

STUDY AREA

Voyageurs National Park (48.50° N, 92.88° W) is an 882 km^2 protected area comprised of a mixture of forested land (61%) and large lakes (39%) along the U.S.-Canada border. Moose are primarily restricted to the Kabetogama Peninsula (Windels 2014), a 300 km^2 roadless area in the center of VNP, and have remained relatively stable since the 1990s with density ranging from 0.14–0.19 moose/km² (Windels 2014). White-tailed deer density in winter during the study ranged between 3–6/km² (Gogan et al. 1997, unpublished data of VNP). Vegetation is a mix of southern boreal and Laurentian mixed conifer-hardwood forests comprised primarily of a mosaic of quaking aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea alba*), white pine (*Pinus strobus*), red pine (*P. resinosa*), jack pine (*P. banksiana*), and black spruce (*Picea mariana*) (Faber-Landgendoen et al. 2007). Soils range from thin, sandy loams over bedrock to poorly draining clays at lower elevations (Kurmis et al. 1986). Beaver-created wetlands and associated seral stages are abundant (Johnston and Naiman 1990). Temperatures vary from −40 to 36 °C, with an average annual temperature of 1.4 °C. Mean annual precipitation is 62 cm, with most precipitation falling between May and September (Kallemeyn et al. 2003).

METHODS

We used the "ecotype"-level vegetation classification derived from the USGS-NPS Vegetation Map (Hop et al. 2001) to select the 10 most common terrestrial ecotypes on the Kabetogama Peninsula to sample for gastropods. We excluded 4 of these because they were too wet to sample with our methodology: poor conifer swamps, rich hardwood swamps, wet meadows, and shrub bogs. The remaining 6 ecotypes comprised 80% of the non-aquatic vegetation communities (Table 1); 4 were dry uplands (rock barrens with trees, northern spruce-fir forests, boreal hardwood forests, and northern pine forests) and 2 wet lowland ecotypes (northern shrub swamp and rich conifer swamp). We randomly selected 5 patches (polygons) within each of the 6 ecotypes within a restricted area to facilitate access to sampling sites (Fig. 1) assuming that these sites were representative of those across the entire Peninsula. At each site we sampled during a single over-night period at approximately 1-month intervals in each of 4 periods: 6–20 June, 29 July–3 August, 18–25 August, and 9–14 September.

Table 1. Area (km²) and % total area covered by each of 6 terrestrial vegetation ecotypes sampled on the Kabetogama Peninsula, Voyageurs National Park (VNP), Minnesota, USA, June-September 2011. Area calculations exclude lakes and ponds. Ecotype classifications are according to the US-National Vegetation Classification System applied to VNP (Hop et al. 2001).

Ecotype	Area (km²)	%
Northern Spruce-Fir Forest	66	23
Boreal Hardwood Forest	62	21
Northern Pine Forest	52	18
Treed Rock Barrens	39	13
Northern Shrub Swamp	8	3
Rich Conifer Swamp	5	2
Total	232	80

We used 0.25 m² cardboard sampling squares (50 × 50 cm) placed on ground vegetation to collect gastropods (Lankester and Peterson 1996, Hawkins et al. 1998, Nankervis et al. 2000, Maskey 2008). We randomly selected a starting sample point and direction within each polygon such that a 100-m sampling transect would fit entirely within the polygon. We placed 10 corrugated cardboard squares on the 100-m transect and verified that all were in the same ecotype. The cardboard was placed directly on the soil or duff layer after rocks and branches were cleared from the sampling site. The cardboard was saturated with water and covered with a 0.36 m² sheet of 3-mm thick clear plastic.

Sheets were set in the morning and retrieved ~24 h later. The wetness of each sheet was estimated as the percentage of the bottom that was visibly damp. All slugs

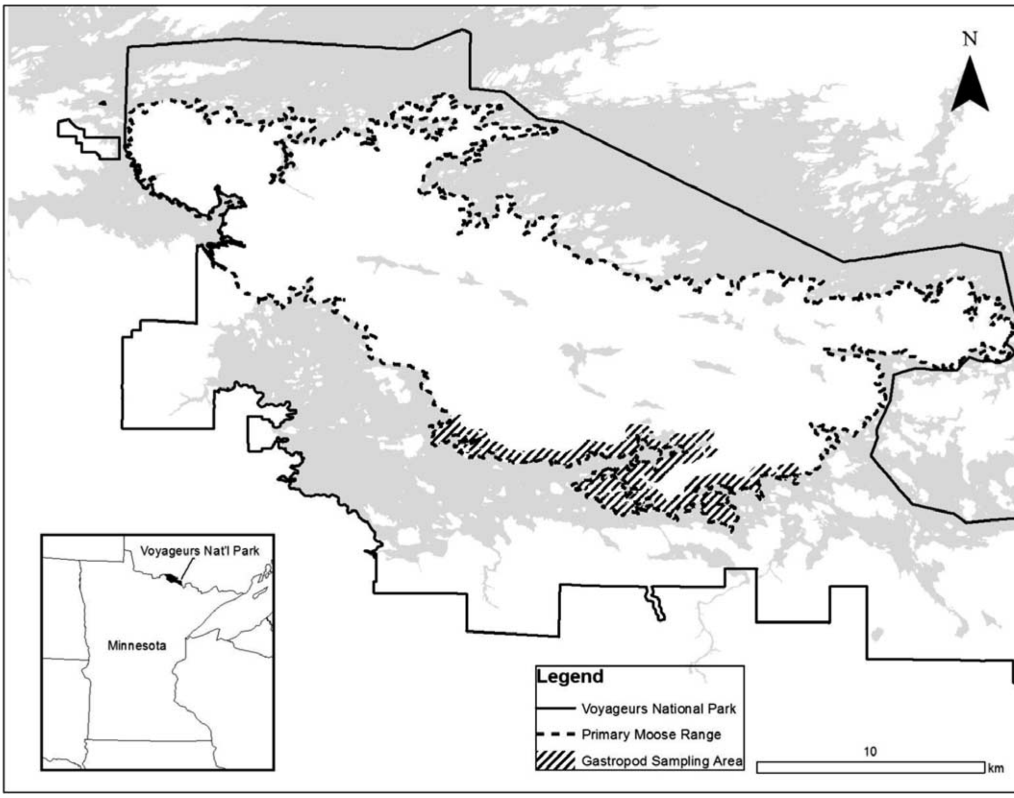

Fig. 1. Primary moose range (dashed line) and terrestrial gastropod sampling area (cross-hatched area) in Voyageurs National Park, Minnesota, USA, 6 July-14 September 2010.

and snails on the underside of the cardboard were collected and stored in plastic jars with damp paper towels. Subsequent identification was to the lowest taxonomic level possible using available keys (Burch 1962, Nekola 2007, J. Nekola, Minnesota Department of Natural Resources, pers. comm.). In 3 cases, we lumped 2 closely related species together that could not be reliably differentiated by morphological characteristics: *Zonitoides nitidus* and *Z. arboreus, Nesovitrea electrina* and *N. binneyana,* and *Euconulus alderi* and *E. fulvous.* We identified potential gastropod vectors of *P. tenuis* based on a literature review (Lankester and Anderson 1968, Gleich et al. 1977, Upshall et al. 1986, Rowley et al. 1987, Platt 1989, Lankester and Peterson 1996, Whitlaw et al. 1996, Nankervis et al. 2000, Lankester 2001).

We considered the 100-m sample transect the sample unit and tested for the effects of ecotype and sample period on abundance of gastropod groups (total gastropods, snails only, slugs only) using factorial ANOVA. We also tested for an interaction between ecotype and sampling period. We used Bonferroni corrections when making post-hoc comparisons between main effects (ecotype and sample period) and set statistical significance at $P = 0.05$.

We obtained GPS locations at 15-min intervals from 11 adult moose (9F:2M) wearing GPS collars to measure habitat use during June-September 2010. Spatial data were displayed using ArcGIS 10.1 with ArcGIS Spatial Analyst (ESRI, Redlands, CA, USA 2012), and home ranges were calculated in the Geospatial Modeling Environment

(2012 Spatial Ecology LLC) running via ArcGIS 10.1 and R 3.0.1. We calculated the proportion of locations in each ecotype for individual moose. We calculated a relative measure of *P. tenuis* transmission risk to moose in different ecotypes by comparing the abundance of gastropods in each ecotype to habitat use in each ecotype. Mean monthly habitat use (i.e., proportion of all locations within an ecotype) varied little from June to September; all differences were <5% between months for any ecotype. We therefore used the mean proportion of use for the entire June-September period to estimate an overall risk of *P. tenuis* infection by ecotype during summer.

We also evaluated variation in relative risk of *P. tenuis* infection to individual moose. Risk Value was calculated by multiplying the proportion of each ecotype used by a moose by the mean density of potential *P. tenuis* gastropod vectors measured in each ecotype. We scaled the Risk Value for each moose to the highest individual Risk Value to compare relative risk of infection among individual moose. Our indices of risk assume that 1) gastropod infection rates (i.e., proportion of gastropods infected with *P. tenuis* larvae) did not vary among gastropod species, among habitat types, or over the sampling time, and 2) the likelihood of a moose ingesting a potentially infected vector gastropod in a given ecotype is proportional to the density of known vectors of *P. tenuis* in that ecotype. Our index of risk does not consider morbidity or mortality for infected moose, because the severity and duration of the infection can be highly variable (Lankester 2002, 2010).

RESULTS

We collected 6,595 gastropods representing 9 families and 25 species (3 slug species and 22 snail species; Table 2), and successfully classified 62% of slugs and 50% of snails. We could not identify 3,116 (47%) of the gastropods because they were damaged beyond recognition during collection and storage, or were juveniles that can be difficult to identify accurately even to the family level (J. Nekola, pers. comm.). The total number of snails/m^2 (including unidentified) increased from July to September in all ecotypes combined (ANOVA, $F_{3,29} = 8.7$, $P < 0.001$). The treed rock barren cover type had the lowest snail density (7.1/m^2) for all sampling periods combined. The northern pine forest and northern spruce-fir forest ecotypes had the most snails for all periods combined, increasing from 7.3 and 10.2 snails/m^2 in July to 23.7 and 22.8 snails/m^2 in September, respectively (Fig. 2).

Overall, slug density was relatively constant over time within each ecotype, and at lower density than snails. Slug density (including unidentified) was more variable over time than snail density (Fig. 3). Slug density in all 4 sampling periods combined was lowest (1.3/m^2) in the rich conifer swamp ecotype and highest in the northern pine (6.2/m^2) and northern spruce-fir forests (6.9/m^2). Northern shrub swamp (3.3/m^2) and rich conifer swamp (1.3/m^2) had lower slug densities than the other 4 ecotypes (ANOVA, $F_{5,29} = 20.88$, $P < 0.001$).

Cardboard wetness increased as the survey progressed (ANOVA, $F_{3,29} = 165.8$, $P < 0.001$); for example, mean wetness was 47% in Survey 1 and 90% in Survey 4. Within ecotypes, cardboard wetness in the treed rock barren ecotype was lower (51%) than in the other 5 ecotypes (range = 75–82%; ANOVA, $F_{5,29} = 44.3$, $P < 0.001$).

Eight of the collected species are known vectors of *P. tenuis* and comprised 32% of the sample. The slug *Deroceras laeve* was the most common vector collected (26% of total captures), was present in every ecotype, and most common in the northern spruce-fir forest ecotype. Two other slug vectors were *Pallifera hemphili* and a *Deroceras* specimen that we could not identify to species, but

Table 2. Composition of terrestrial gastropods collected in Voyageurs National Park, Minnesota, USA, June-September 2011. Gastropod species were identified to the lowest taxonomic level possible; 62% of slugs and 50% of snails were classified.

Group	Family	Species	Count	% Total Captures
P. tenuis Vectors				
Slug	Limacidae	*Deroceras laeve*	906	26.0
Slug	Limacidae	*Deroceras sp.* (but not *D. leave*)	13	0.4
Slug	Philomycidae	*Pallifera hemphili*	6	0.2
Snail	Endodontidae	*Discus cronkhitei*	55	2.0
Snail	Strobilopsidae	*Strobilops* spp.	145	4.0
Snail	Valloniidae	*Cochlicopa sp.*	6	0.2
Snail	Zonitidae	*Zonitoides (nitidus+arboreas)*	159	4.6
Total			1290	37.4
Non-vectors				
Snail	Endodontidae	*Helicodiscus parallelus*	7	0.2
Snail	Endodontidae	*Punctum californicum*	7	0.2
Snail	Endodontidae	*Punctum minutissimum*	2	<0.1
Snail	Endodontidae	*Punctum* spp.	4	0.1
Snail	Oxychilidae	*Nesovitrea (electrina+binneyana)*	105	3.0
Snail	Pupillidae	*Columella simplex*	6	0.2
Snail	Pupillidae	*Gastrocopta pentodon*	6	0.2
Snail	Pupillidae	*Gastrocopta sp.*	11	0.3
Snail	Pupillidae	*Vertigo* spp.	319	9.0
Snail	Pupillidae	*Unknown*	143	4.0
Snail	Succineidae	*Oxyloma retusa*	19	0.5
Snail	Valloniidae	*Cochlicopa lubricella*	11	0.3
Snail	Valloniidae	*Zoogenetes harpa*	62	2.0
Snail	Zonitidae	*Euconulus (alderi + fulvous)*	638	18.0
Snail	Zonitidae	*Guppya sterkii*	6	0.2
Snail	Zonitidae	*Striatura milium*	29	0.8
Snail	Zonitidae	*Striatura exigua*	7	0.2
Snail	Zonitidae	*Striatura ferrea*	6	0.2
Snail	Zonitidae	*Vitrina limpida*	326	9.0
Snail	Zonitidae	Unknown	461	13.0
Total			2175	61.4

assumed was a *P. tenuis* vector like its congener *D. leave*. The snails *Discus cronkhitei, Zonitoides nitidus+arboreas, Strobilops* spp., and *Cochlicopa* sp., known vectors of *P. tenuis,* were ~11% of the sample and found across all surveys and sample sites (Table 2).

Risk of *P. tenuis* infection was highest in northern spruce-fir forests (Fig. 4). The northern spruce-fir ecotype had the highest use by moose (35% of total locations) and also had the second highest estimated density of *P. tenuis* vectors. Treed rock barrens had the fourth highest use by moose (8%)

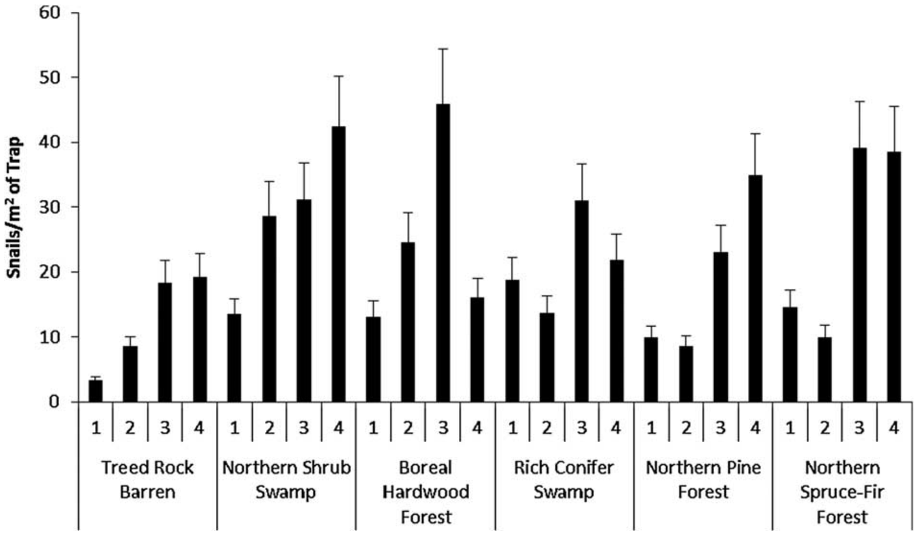

Fig. 2. Mean (+SE) number of snails/m² (including unidentified) measured in each of 6 ecotypes for a single over-night period in each of 4 sampling periods in June-September, 2011 in Voyageurs National Park, Minnesota, USA. Sample periods were: Survey 1 = 6–20 June, Survey 2 = 29 July – 3 August, Survey 3 = 18–25 August, Survey 4 = 9–14 September.

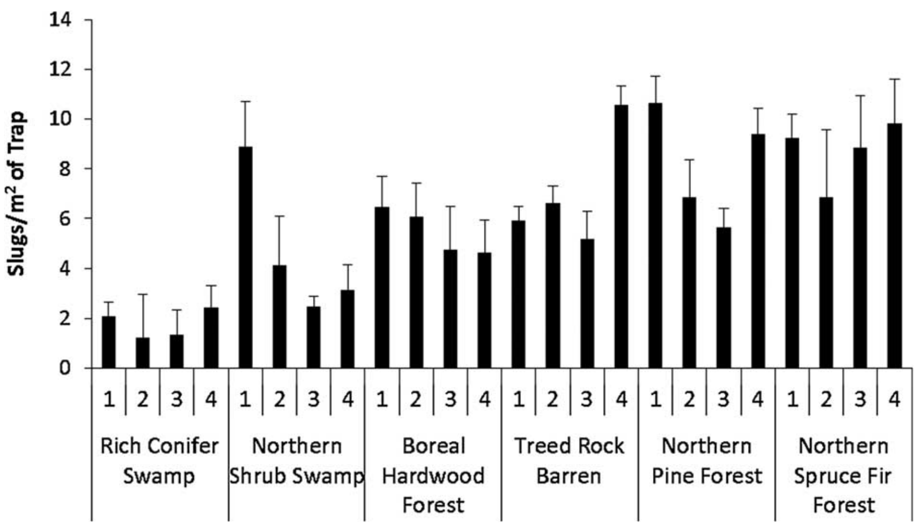

Fig. 3. Mean (+SE) number of slugs/m² (including unidentified) measured in each of 6 ecotypes for a single over-night period in each of 4 sampling periods in June-September, 2011 in Voyageurs National Park, Minnesota, USA. Sample periods were: Survey 1 = 6–20 June, Survey 2 = 29 July – 3 August, Survey 3 = 18–25 August, Survey 4 = 9–14 September.

and the third highest *P. tenuis* vector density, suggesting moderate risk. Boreal hardwood forests were also a moderate risk ecotype based on their relatively high use and low vector density. Rich conifer swamps and northern shrub swamps were low risk

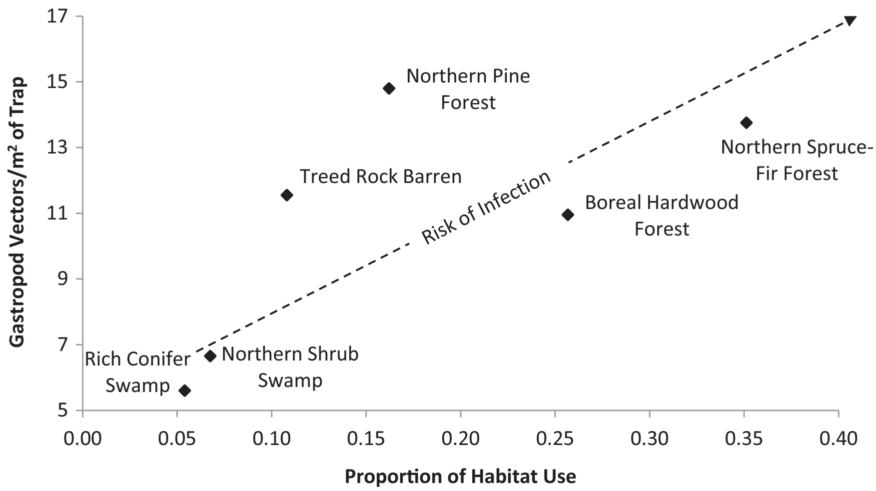

Fig. 4. Relative risk of moose encountering *P. tenuis* gastropod vectors in 6 ecotypes in Voyageurs National Park, Minnesota, USA, July-September 2010.

ecotypes because of their relatively low use (5% and 7%) and low density of *P. tenuis* vectors (Fig. 4).

Moose displayed variability in individual risk of infection as a result of differential habitat use. Ten of 11 moose had Relative Risk scores of 0.68–1.0, and Relative Risk differed by ≤32% for the majority of moose. Moose V09 was an exception as it spent little time in gastropod rich habitats and had a much lower risk of infection (0.21) relative to the other moose (Table 3).

DISCUSSION

Gastropod density, and more specifically density of known vectors of *P. tenuis*, differed among the ecotypes and sample periods. Similar to previous studies, ecotypes of mixed conifer-deciduous forest types had the highest gastropod densities (Gleich et al. 1977, Kearney and Gilbert 1978, Nankervis et al. 2000). The increasing density of gastropods and potential *P. tenuis* vectors from summer to fall is also consistent with previous studies in northern Minnesota (Lankester and Peterson 1996). *D. laeve* was the most abundant gastropod found in our study area, and is likely the most important vector of *P. tenuis*. Most larvae in infected gastropods are presumably in the infective stage (i.e., third stage) by early July (Lankester and Peterson 1996) corresponding to our sampling period between mid-June and September.

The cardboard sampler method is meant to provide a relative measure of gastropod diversity and abundance, and it is critical that they be as uniform as possible in shape, thickness, and wetness. All were saturated with water at the time of deployment but dried at different rates depending on habitat features (e.g., soil moisture, rockiness, exposure) and weather conditions (e.g., dry and windy vs. calm and humid). Cardboard wetness varied from 0–100% at collection and this wide variation could skew the estimates of gastropod abundance because they are less likely to be found on dry cardboard (unpublished data, VNP).

Variation in cardboard wetness could be minimized by distributing the cardboard after the warmest part of the day and checking them before the warmest part of the next day, which would be especially important in the longer and warmer days in July and early August. Past studies indicate lower

Table 3. Proportional habitat use and individual risk of moose encountering *P. tenuis* infected gastropods in the Kabetogama Peninsula, Voyageurs National Park, Minnesota, USA, June-September 2010. Risk value is calculated by multiplying the proportion of each ecotype used by a moose by the mean density of *P. tenuis* gastropod vectors measured in each ecotype. The Relative Index of Risk is the Risk Value scaled to the highest Risk Value found for an individual moose in 2010 (i.e., Moose V05).

	Proportion Habitat Use							
Moose #	Northern Pine Forest	Northern Spruce- Fir Forest	Treed Rock Barren	Boreal Hardwood Forest	Northern Shrub Swamp	Rich conifer Swamp	Risk Value	Relative Index of Risk
V05	0.43	0.18	0.02	0.24	0.00	0.03	9.50	1.00
V06	0.42	0.10	0.02	0.17	0.03	0.05	8.96	0.94
V07	0.09	0.34	0.11	0.18	0.07	0.04	8.91	0.94
V14	0.05	0.35	0.14	0.19	0.10	0.04	8.76	0.92
V07	0.04	0.37	0.10	0.18	0.06	0.03	7.80	0.82
V10	0.05	0.33	0.10	0.19	0.06	0.03	7.66	0.81
V18	0.07	0.19	0.26	0.19	0.02	0.00	7.64	0.80
V17	0.13	0.25	0.08	0.18	0.03	0.02	7.44	0.78
V12	0.10	0.32	0.03	0.21	0.06	0.05	7.23	0.76
V08	0.01	0.37	0.00	0.27	0.02	0.01	6.49	0.68
V09	0.00	0.17	0.00	0.13	0.09	0.11	2.04	0.21

gastropod abundances in early summer (Lankester and Anderson 1968, Kearney and Gilbert 1978, Lankester and Peterson 1996), and although these studies did not report the relative wetness of cardboard sheets, they may be biased low if sheets were drier in early summer. Cardboard samplers may underestimate the total density of gastropods in an area, as the number of gastropods in the soil underneath cardboard samplers has been reported higher than those attached to the cardboard samplers (Hawkins et al. 1998).

By combining information about gastropod density and relative habitat use, we assessed the relative risk of *P. tenuis* infection for moose in different habitat types (Fig. 4). We likewise calculated Risk Values for individual moose (Table 3). These methods can also be used to compare risk of infection between different geographic areas or populations. However, we caution that the assumptions associated with our methods need to be considered carefully because seasonal variation of infection rates in gastropod hosts is not well understood (Lankester and Anderson 1968, Kearney and Gilbert 1978, Lankester and Peterson 1996). High white-tailed deer density has been correlated with increased infection rates of gastropods (Lankester and Peterson 1968) and moose (Whitlaw and Lankester 1994a) at larger spatial scales. A recent study found no correlation between white-tailed deer abundance and *P. tenuis* infection at smaller spatial scales within VNP (VanderWaal et al. 2014), although the range of deer abundance was limited across sites.

Risk of *P. tenuis* infection varies among individual moose because of differences in habitat use within respective home ranges. It will also be influenced by landscape composition and the availability of different habitats within an area. For example, the western half of the Kabetogama Peninsula has more area covered by the higher risk boreal hardwood and northern spruce-fir ecotypes, and conversely, the eastern half of the park contains more of the drier, low risk treed rock barrens and northern pine ecotypes. VanderWaal et al. (2014) found that *P. tenuis* infection rates in white-tailed deer increased as the proportion of vector-rich habitats such as mixed conifer-hardwood forest increased within a local area.

While our methods only considered coarse habitat use in our Risk Index, moose behavior within individual ecotypes is presumably also important. Moose may prefer to bed in certain ecotypes (e.g., in lowland habitats in hot weather) and feed in others (Peek 1997), and even if gastropods are abundant in certain ecotypes, the risk of *P. tenuis* infection should be less in areas less preferred for foraging. Risk of infection may also be affected by individual preferences for forage choice, previous exposure to *P. tenuis*, health status, genetics, body mass/longevity (Ezenwa et al. 2006), and other factors not considered here.

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