Science Advances

Supplementary Materials for

Spatial compartmentalization: A nonlethal predator mechanism to reduce parasite transmission between prey species

L. Gustavo R. Oliveira-Santos*, Seth A. Moore, William J. Severud, James D. Forester, Edmund J. Isaac, Yvette Chenaux-Ibrahim, Tyler Garwood, Luis E. Escobar, Tiffany M. Wolf

*Corresponding author. Email: gu_tapirus@hotmail.com

This PDF file includes:

Extended methods
Supplementary results
Figs. S1 to S3
Tables S1 to S3

Extended methods

Parelaphostrongylus tenuis life cycle

Parelaphostrongylus tenuis is a neurotropic nematode in which the white-tailed deer (hereafter deer) is the only vertebrate definitive host (deer prevalence >90%; (27)). It infects and reproduces in the deer's meningeal tissue, laying eggs in the central nervous system and then translocated to lungs, where they hatch (*23*). Larvae (first-stage) are coughed up, swallowed, and go through the gastrointestinal tract, where they are shed during defecation. First-stage larvae, occurring on feces or soil, penetrate the bodies of terrestrial gastropods (snails and slugs; the invertebrate intermediate host) where they develop from L1 to L3 larvae. Deer become infected by incidentally ingesting vegetation with gastropods infected with third-stage larvae (L3), giving continuity to the parasite cycle (Figure 1). Infection in deer provokes immune response, but clinical signs of infection are rarely reported. *P. tenuis* can abnormally infect deeper neurological tissues of other ungulates of economic and conservation concern, such as moose, elk (*Cervus canadensis*), caribou (*Rangifer tarandus*), and mule deer (*Odocoileus hemionus*). Central nervous system damage causes neurological impairment and can lead to death in these aberrant hosts (*62*)(symptoms: motor deficiency, hindquarters weakness, incapacity keeping upright and loss of fear). As *P. tenuis* does not reproduce in and is not transmitted by these species, they are considered dead-end hosts. Because aberrant hosts do not contribute to transmission, range overlap with white-tailed deer is essential for *P. tenuis* infection in other ungulate hosts.

Regarding weather, absence of snow, milder temperatures, and increased precipitation favor first-stage larvae survival on deer feces and in leaf litter, and abundance, mobility, and survival of invertebrate hosts (*26, 51*). Thusly, summer and spring favor encounter rates between vertebrate and invertebrate hosts. Furthermore, the shedding rate of larvae in deer feces is higher in late winter and spring (*28*). Contrastingly, deer movement during summer among migratory populations should decrease deer density and, consequently, diminish parasite prevalence among invertebrate hosts (*26, 79*). Regarding habitats, shaded and wet areas are expected to favor larvae survival on feces and soil, and survival, mobility, and abundance of invertebrate hosts. Therefore, parasite prevalence in gastropods have been detected six times higher in forested, wet habitats than dry upland forest (*50*). Conflicting evidence has demonstrated swamp conifer forest with the lowest gastropod abundance among covertypes (*51*), and upland conifer forest and upland shrub with higher parasite prevalence in gastropods than lowland coniferous or deciduous forest (*52*).

Study area and species

We conducted this study in and around the Grand Portage Indian Reservation of the Lake Superior Band of Chippewa in northeastern Minnesota, USA, in the northern superior uplands forest region located around northwest of Lake Superior (4°50'N, 92°8'W). The reservation (227 km^2) is bordered to the north by the Pigeon River and Ontario, Canada; to the southeast by thirty-nine km of Lake Superior shoreline; and to the west by a mix of federal, state, and private lands. The landscape is characterized by a matrix of forested stands and wetlands (e.g. bogs, lakes and ponds), and dominated by upland conifer, upland deciduous, and mixed conifer-deciduous forests (*59*). These forest stands are part of the south-north transitional gradient between US northern hardwoods and Canadian boreal forest. Dominant tree species include white spruce (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*). Forest stands are usually disturbed by fire and are subject to timber harvest. Topographic relief is smooth mainly around Lake Superior's shore with few rocky outcrops westward (around lakes and rivers). Climate is mid-continental, with long severe winters (average temperature for January = -13.1°C) and short warm summers (average temperature for July = 18.9°C), as well as moderate

precipitation (www.ncdc.noaa.gov for Duluth Station). Snow cover typically occurs from November through April.

In northeastern Minnesota, moose co-occur with white-tailed deer and adults of both species are primarily preyed upon by grey wolves (*Canis lupus*) (*31*, *32*). State-permitted harvest is prohibited for moose (since 2012 due to population decline), but a limited tribal harvest resumed in 2016. Wolves were federally protected within Minnesota (but were legally harvested in 2013-2014 when delisted) during the time of this study; deer are harvested annually. Overall moose density across the region is ~ 0.26 individuals/km² (90% CI = ~0.21–0.34; (*24*)), and wolf density is ~0.03 individuals/km² (*61*). Deer density is about 0.76–3.80 individuals/km² (*60*), with densities decreasing from Lake Superior's shore westward due to migratory behavior by the population (*33*). Deer are spatially aggregated at Lake Superior's shore during winter (November through March), performing fast, long northern displacements to reach summer range areas west of the lake shore, usually crossing into Canada.

Supplementary results
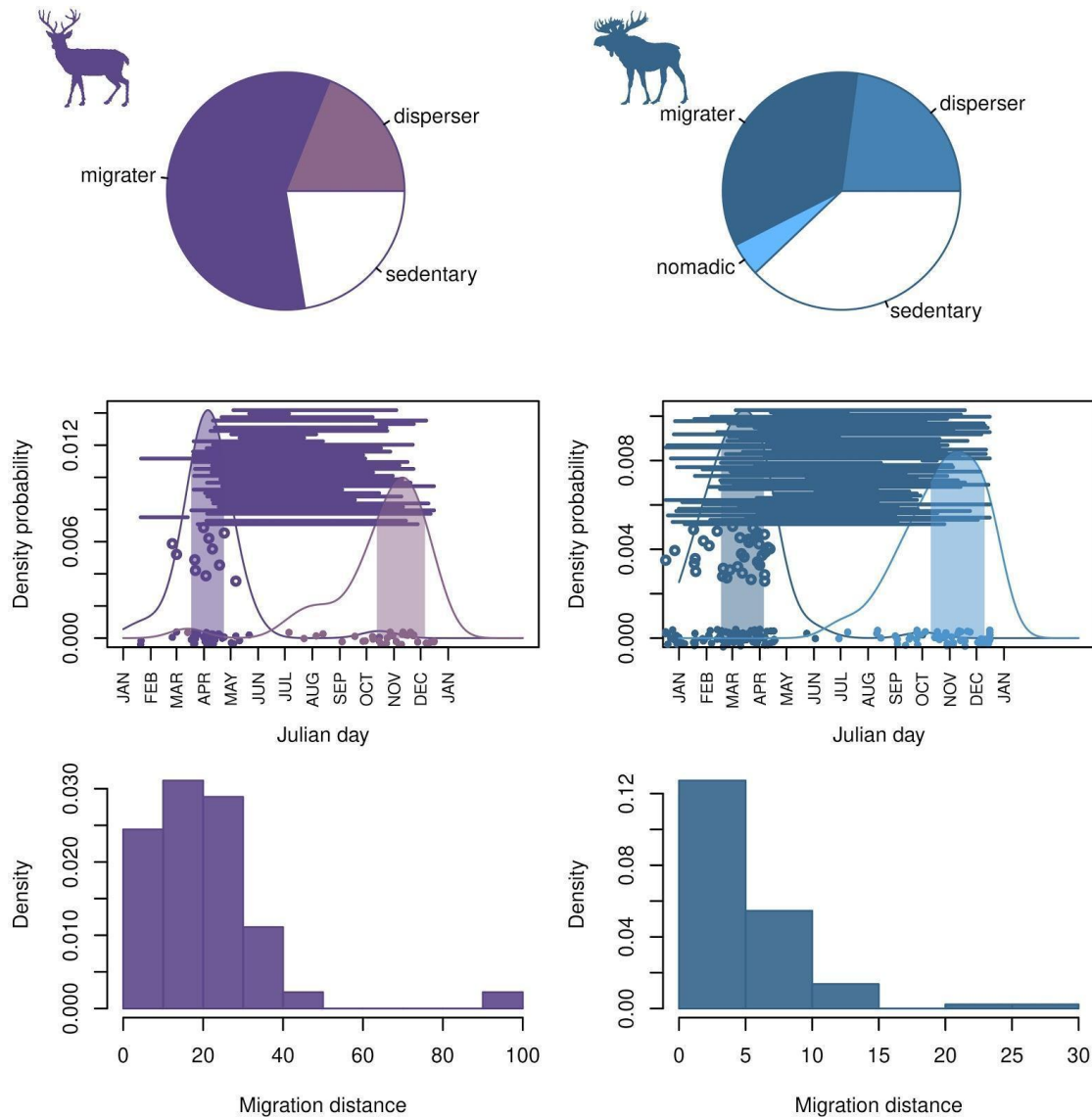
Figure S1. Migration phenology of vertebrate hosts (white-tailed deer, *Odocoileus virginianus,* and moose, *Alces alces*) in and around Grand Portage, Minnesota, USA. Top panel: Proportion of individuals classified in each movement syndrome (nomadic, sedentary, migrator or disperser). Central panel: Circular kernel density probability of departure date in spring (gray curve) and fall migration (black curve). Bottom points depict estimated migration dates for each individual; horizontal gray lines indicate time range when individuals settled in summer range; open gray circles depict dates of dispersal for individuals classified as dispersers. Bottom panel: Histograms of migration distances in kilometers.
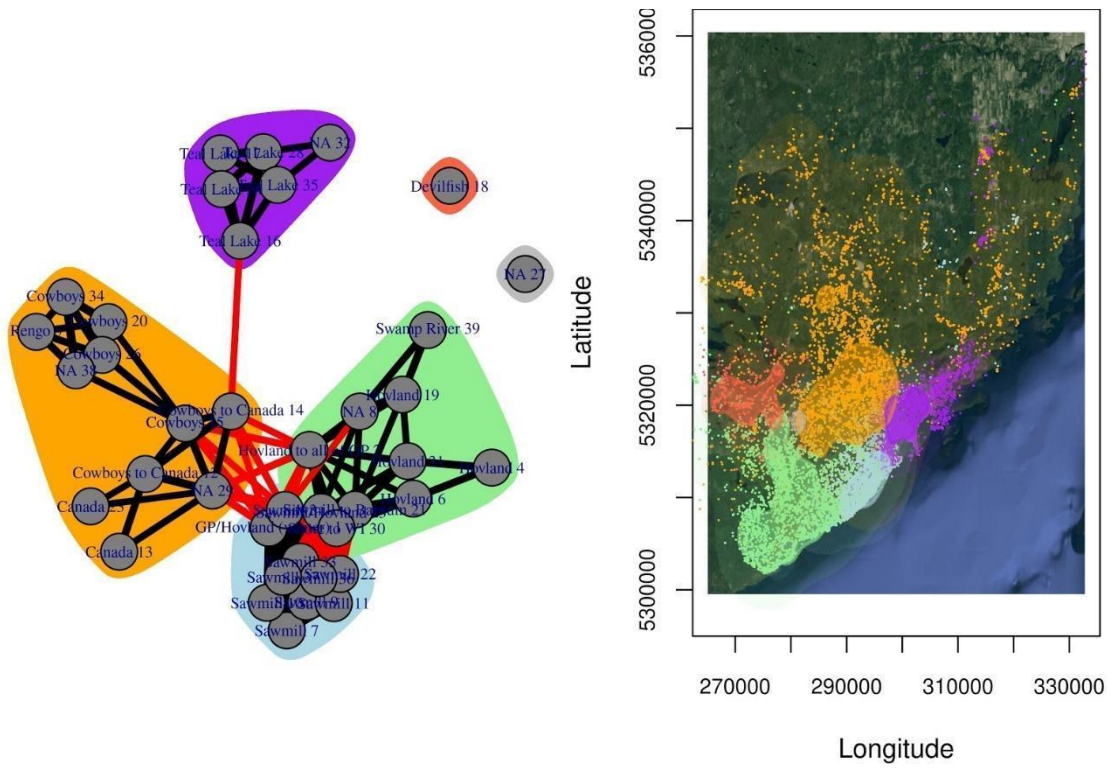
Figure S2. Results of social network clustering based on wolves' home ranges to identify number of packs and pack composition. Left panel: Classification of wolf packs. Right panel: Spatial distribution of pack territories. Points depict location and polygons Kernel 95% and Kernel 50% for each pack territory.
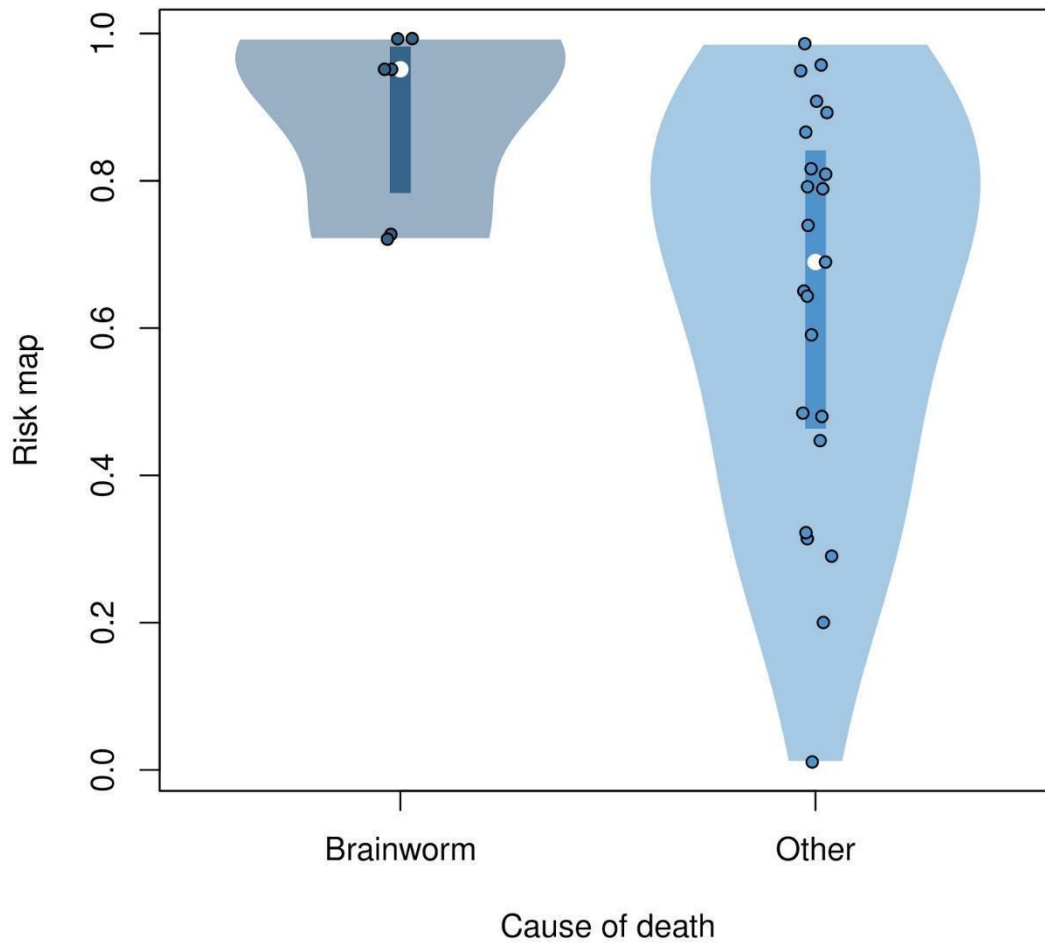
Figure S3. Violin plot of observed *P. tenuis* spillover risk map values calculated for trajectories of individuals who died with *P. tenuis* infection *versus* those that died of other causes. Dark-color dots are observations, white dots are means, vertical rectangles are standard deviations around means, and violins depict nonparametric density probability of observed values.

Table S1. Ranking of Step Selection Function models for white-tailed deer (*Odocoileus virginianus*) and moose (*Alces alces americanus*). k = number of parameters; Loglik = Log-Likelihood; AICc = corrected Akaike Information Criteria; ΔAICc = difference between model's AICc and best model's AICc; w = Akaike weights.

Species	Model	k	LogLik	AICc	ΔAICc	w
Deer	Full	29	-393119.3	786296.6	0.00	1
	Habitat-predator	15	-393146.3	786322.5	25.92	0
	Habitat-time	21	-393183.0	786408.0	111.41	0
	Habitat	7	-393204.9	786423.8	127.19	0
Moose	Full	29	-854279.1	1708616	0.00	1
	Habitat-time	21	-854317.6	1708677	60.96	0
	Habitat-predator	15	-854527.2	1709084	468.17	0
	Habitat	7	-854566.9	1709148	531.60	0

Table S2. Estimated coefficients, and their 95% confidence intervals, of the four SSF models for each species (deer and moose).

Habitat model

Covariate	Deer			Moose		
	Lower limit	Upper limit	Estimate	Lower limit	Upper limit	Estimate
Elevation	0.016	0.115	0.066	-0.084	-0.015	-0.049
Mixed forest	0.013	0.092	0.053	0.210	0.271	0.241
Deciduous forest	0.036	0.127	0.082	0.182	0.243	0.212
Open areas	0.104	0.206	0.155	0.360	0.461	0.411
Urban areas	-0.753	-0.601	-0.677	-0.831	-0.554	-0.692
Wetlands	-0.310	-0.147	-0.228	-0.004	0.062	0.029
Water bodies	-1.093	-0.786	-0.940	-0.310	-0.172	-0.241

Habitat-season model

Covariate	Deer			Moose		
	Lower limit	Upper limit	Estimate	Lower limit	Upper limit	Estimate
Elevation	-0.062	0.101	0.020	0.206	0.368	0.287
Mixed forest	-0.052	0.070	0.009	0.177	0.321	0.249
Deciduous forest	-0.042	0.098	0.028	0.036	0.182	0.109
Open areas	0.097	0.235	0.166	-0.073	0.186	0.056
Urban areas	-0.720	-0.516	-0.618	-0.797	-0.199	-0.498
Wetlands	-0.345	-0.137	-0.241	-0.471	-0.308	-0.390
Water bodies	-1.167	-0.558	-0.863	-1.832	-1.126	-1.479
Elevation:season-migration	0.087	0.392	0.240	-0.540	-0.225	-0.382
Elevation:season-summer	-0.083	0.134	0.026	-0.501	-0.321	-0.411
Mixed forest:season-migration	-0.139	0.105	-0.017	-0.005	0.251	0.123
Deciduous forest:season-migration	-0.073	0.204	0.065	0.035	0.305	0.170
Open areas:season-migration	-0.055	0.234	0.090	0.068	0.475	0.272
Urban areas:season-migration	-0.123	0.315	0.096	-0.800	0.310	-0.245

Wetlands:season-migration	-0.515	0.073	-0.221	0.131	0.414	0.273
Water bodies:season-migration	-0.431	0.616	0.093	0.164	1.184	0.674
Mixed forest:season-summer	-0.006	0.170	0.082	-0.113	0.047	-0.033
Deciduous forest:season-summer	-0.015	0.187	0.086	0.039	0.201	0.120
Open areas:season-summer	-0.199	0.038	-0.080	0.297	0.582	0.440
Urban areas:season-summer	-0.380	-0.029	-0.205	-0.592	0.092	-0.250
Wetlands:season-summer	-0.108	0.267	0.080	0.435	0.615	0.525
Water bodies:season-summer	-0.471	0.255	-0.108	0.995	1.716	1.356

Habitat-predator model

Covariate	Deer			Moose		
	Lower limit	Upper limit	Estimate	Lower limit	Upper limit	Estimate
Deciduous forest	0.062	0.165	0.114	0.179	0.241	0.210
Open areas	0.055	0.185	0.120	0.373	0.476	0.424
Urban areas	-0.740	-0.567	-0.654	-0.832	-0.554	-0.693
Wetlands	-0.227	0.021	-0.103	-0.009	0.057	0.024
Water bodies	-0.997	-0.684	-0.840	-0.309	-0.170	-0.240
Elevation	0.015	0.114	0.065	-0.096	-0.026	-0.061
Predation risk	0.167	0.438	0.303	-0.110	-0.025	-0.067
Elevation:Predation risk	0.040	0.145	0.093	-0.082	-0.020	-0.051
Mixed forest:Predation risk	-0.141	-0.041	-0.091	-0.028	0.035	0.004
Deciduous forest:Predation risk	-0.225	-0.114	-0.170	0.002	0.070	0.036
Open areas:Predation risk	0.010	0.139	0.074	-0.103	-0.005	-0.054
Urban areas:Predation risk	-0.047	0.123	0.038	-0.189	0.106	-0.042
Wetlands:Predation risk	-0.276	-0.030	-0.153	-0.017	0.051	0.017

Water bodies:Predation risk	-0.014	0.317	0.151	0.132	0.251	0.192

Full model

Covariate	Deer			Moose		
	Lower limit	Upper limit	Estimate	Lower limit	Upper limit	Estimate
Elevation	-0.201	-0.019	-0.110	0.186	0.350	0.268
Mixed forest	0.016	0.173	0.094	0.174	0.318	0.246
Deciduous forest	0.100	0.277	0.188	0.030	0.176	0.103
Open areas	-0.010	0.187	0.088	-0.045	0.220	0.087
Urban areas	-0.738	-0.463	-0.601	-0.794	-0.196	-0.495
Wetlands	-0.223	0.073	-0.075	-0.485	-0.321	-0.403
Water bodies	-1.418	-0.672	-1.045	-1.832	-1.127	-1.480
Predation risk	0.211	0.489	0.350	-0.122	-0.038	-0.080
Elevation:season-summer	0.131	0.398	0.264	-0.491	-0.310	-0.401
Elevation:season-migration	0.207	0.523	0.365	-0.535	-0.219	-0.377
Mixed forest:season-migration	-0.190	0.063	-0.063	-0.004	0.252	0.124
Deciduous forest:season-migration	-0.192	0.093	-0.049	0.037	0.307	0.172
Open areas:season-migration	-0.004	0.293	0.145	0.040	0.451	0.246

Urban areas:season-migration	-0.106	0.337	0.116	-0.839	0.284	-0.277
Wetlands:season-migration	-0.575	0.019	-0.278	0.141	0.425	0.283
Water bodies:season-migration	-0.246	0.851	0.302	0.164	1.184	0.674
Mixed forest:season-summer	-0.119	0.093	-0.013	-0.113	0.047	-0.033
Deciduous forest:season-summer	-0.265	-0.021	-0.143	0.042	0.204	0.123
Open areas:season-summer	-0.139	0.136	-0.002	0.270	0.558	0.414
Urban areas:season-summer	-0.393	0.048	-0.173	-0.596	0.089	-0.254
Wetlands:season-summer	-0.146	0.232	0.043	0.446	0.627	0.536
Water bodies:season-summer	-0.215	0.803	0.294	0.999	1.719	1.359
Elevation:Predation risk	0.099	0.225	0.162	-0.067	-0.004	-0.035
Mixed forest:Predation risk	-0.152	-0.033	-0.092	-0.022	0.040	0.009
Deciduous forest:Predation risk	-0.275	-0.142	-0.209	0.006	0.074	0.040
Open areas:Pre dation risk	0.003	0.152	0.078	-0.079	0.021	-0.029
Urban areas:Predation risk	-0.119	0.094	-0.013	-0.195	0.107	-0.044
Wetlands:Predation risk	-0.305	-0.053	-0.179	0.008	0.076	0.042
Water bodies:Predation risk	0.009	0.480	0.245	0.148	0.269	0.208

Table S3. Original NLCD and LCC covertypes and aggregated classes.

Class	NLCD Covertype code	LCC Covertype code
Water bodies	11	20
wetlands	90, 97	81, 82
Coniferous forest	42	211
Deciduous forest	41	220, 221
Mixed forest	43	230-231, 233
urban/developed area	21-24	34

Herbaceous (NLCD: 31, 71 and 81; LCC: 30-33 and 100), shrubs (NLCD: 52; LCC: 8), and crops (NLCD: 82; LCC: 121-122) were very rare or absent across our study area, and therefore not considered for analyses.