

Geospatial analysis of giant liver flukes among moose: effects of white-tailed deer

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Abstract Natural infections of giant liver flukes (*Fascioloides magna*) occur primarily in cervids and bovids. In northeastern North America, a common definitive host for giant liver flukes is the white-tailed deer (*Odocoileus virginianus*). Giant liver flukes cannot reproduce in moose (*Alces alces*) and eventually die, but only after causing extensive tissue damage in the liver. We used data on the occurrence of giant liver flukes in adult moose collected between 1972 and 2000 from northeastern Minnesota, USA. These data were recorded by 93 km² sampling units (square grid of 9.66 km on each side). Sample sizes varied between 0 and 45 adult moose examined per sampling unit. We fitted a second-order global polynomial model to adjust for trends in the occurrence of flukes across the study area, modeled the de-trended data using a circular semi-variogram model, and finally kriged our data, arriving at a

predicted response surface for the occurrence of liver flukes in moose. Correlational analyses indicated that the occurrence of liver flukes in moose was influenced more by the density of white-tailed deer based on rates of hunter harvest ($r=0.54$) than was the proportion of wetland habitats ($r=0.25$). Ordinary least-squares multiple regression ($R_{\text{adj}}=0.29$, $\text{AIC}_c=795.3$) documented a strong relationship between the occurrence of liver flukes in moose and population density of white-tailed deer ($p<0.001$) but a weaker relationship for wetland habitats ($p=0.16$). A geographically weighted multiple regression produced a stronger relationship ($R_{\text{adj}}=0.60$, $\text{AIC}_c=765.7$). Disease maps, as we developed here, are a useful geospatial tool that has relevance for understanding disease processes in moose that may be extended to other mammals.

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William Peterson is now retired from the Minnesota Department of Natural Resources, and Murray Lankester is retired from Lakehead University.

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Introduction

Moose (*Alces alces*) are beset by a variety of diseases, parasites, and pests (Anderson and Lankester 1974; Lankester 1987; Lankester and Samuel 1987; Bowyer et al. 2003 for reviews). One of these parasites, the giant liver fluke (*Fascioloides magna*), is reported from as far south as Florida, USA, to as far north as the Labrador Peninsula, Canada, but its distribution across the North American continent is otherwise spotty and discontinuous (Pybus 2001). The occurrence of this parasite of large herbivores depends on the presence of a competent cervid host, suitable species of aquatic snails (genus *Lymnaea*), and adequate, persistent wetland habitat for transmission to occur (Maskey 2011). Infection occurs when larvae from snails are inadvertently eaten with aquatic vegetation by foraging ungulates. In the liver, *F. magna* occur in pairs within fibrous capsules

formed by the inflammatory response of the host (Pybus 2001). In normal hosts (white-tailed deer, *Odocoileus virginianus*; North American elk, *Cervus elaphus*; and caribou, *Rangifer tarandus*), capsules remain open to bile ducts and eggs of this parasite are passed in feces of the host. Prevalence of infection is lowest in young animals and plateaus in older age classes. In abnormal hosts (e.g., domestic cattle and moose), flukes migrate extensively in the liver and an intense inflammatory response results in diffuse fibrosis, thick-walled closed capsules, and the eventual death of worms. Eggs are seldom, if ever, passed by abnormal or dead-end hosts such as moose (Lankester 1974; Wobeser et al. 1985; Foreyt & Todd 1976).

Conspicuous tissue damage often seen in the liver of moose, has led authors to suggest that the parasite may cause death, particularly of nutritionally stressed animals (Pybus 2001; Lankester and Samuel 1987). Recently, Murray et al. (2006) concluded that the giant liver fluke was a major factor in the decline of moose in northwestern Minnesota, USA. This conclusion, however, has been placed in doubt by studies by Maskey (2011) of a similar moose decline in adjacent North Dakota, USA, where flukes were less prevalent, and by Lankester (2009) and Lankester and Foreyt (2011), who reported no noticeable effect of liver flukes on experimentally infected young and yearling moose observed for up to 16 months of age. Analyzing the spatial distribution of infected moose upon the landscape, in relation to factors that influence rates of infection are important steps in better understanding effects of giant liver flukes on moose populations.

Our first objective was to develop a geospatial model that smoothed our empirical data and allowed us to predict the occurrence of giant liver flukes in moose across townships (93 km² sampling units) for which we lacked data. Our second objective was to examine the relationship between the occurrence of flukes in moose and population densities of white-tailed deer, a definitive host, as well as the influence of wetland zones, which were suitable habitat for

snails. We hypothesized that there would be spatial structure to the occurrence of moose with liver flukes, either because of variation in the density of white-tailed deer, or because of differences in the habitat necessary to support the intermediate host of the fluke. We further predicted that the density of white-tailed deer, a normal definitive host for the fluke, would be positively correlated with the occurrence of giant liver flukes in moose.

Materials and methods

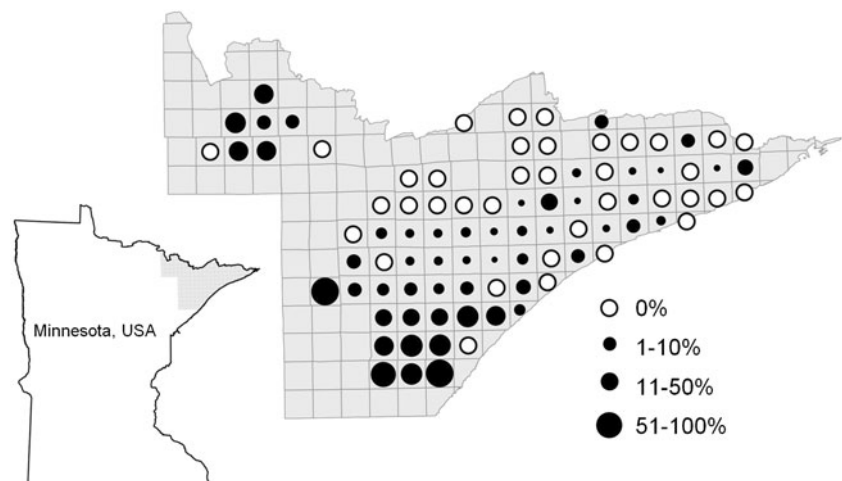
Study area

Our study area encompassed approximately 18,000 km² of northeastern Minnesota, USA, including the counties of Cook, Lake, and St. Louis (Fig. 1). This area is bordered to the north by the Canadian Province of Ontario and to the southeast by Lake Superior. Moose in northeastern Minnesota have slowly declined over time (Lenarz et al. 2010).

Precambrian bedrock lies beneath Pleistocene glacial till (Leverett and Sardeson 1932) of variable depth with scattered bedrock outcrops. Soils range from clay, clay loam, and sandy loam to peat (Grigal and Arneman 1970) and are commonly deeper in the southern portion of the area (Peek et al. 1976). Elevation ranges from 183 m above mean sea level at Lake Superior to 701 m on Eagle Mountain in Cook County. A southeast facing hillside of gentle to moderate slope rises to approximately 200 m above Lake Superior in most locations. Terrain in the remainder of the area varies from flat to gently rolling hills. This heavily forested area is widely known for its numerous lakes but also contains many ponds, streams, swamps, and bogs.

Climate is cool temperate (Hovde 1941). Weather records from 1972 to 1999 (Minnesota Department of Natural Resources, Section of Wildlife, Grand Marais, USA) show that temperatures are moderated by lake effects resulting in

Fig. 1 Study area in northeastern Minnesota, USA. Each square grid cell is a single township (9.66×9.66 km). Size of black symbols reflect infection rate of giant liver flukes in moose. Open circles denote 0 % occurrence; blank townships represent no available data



those at Grand Marais, which is along the shore of Lake Superior, being cooler during summer and warmer during winter than those at Poplar Lake, 37 km inland (Appendix 1). Average annual precipitation at Grand Marais (1972–1999) was 62 cm. Snow generally covers the ground from mid-November until late March to early April along the shore, and until mid-April to early May inland. Mean yearly maximum depth of snow (winter 1969–1970 through winter 1999–2000) was 54 cm at Grand Marais, and 82 cm at a snow-depth measuring site 10 km inland. Additional weather information has been reported for northeastern Minnesota by Van Ballenberghe et al. (1975), Peek et al. (1976), and Nelson and Mech (1981).

Vegetative cover types vary greatly. Upland areas are dominated by stands of aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and mixtures of those trees. A narrow band of sugar maple (*Acer saccharum*) occurs parallel to, and a few kilometers inland from Lake Superior. Logging of the area began in the 1890s and was focused on red pine (*Pinus resinosa*), white pine (*Pinus strobus*), and white spruce; few stands of red and white pine remain, but scattered individual trees of both species occur across much of the area as a “super canopy” (Peek et al. 1976). Lowlands are forested by black ash (*Fraxinus nigra*), black spruce (*Picea mariana*), tamarac (*Larix laricina*), and white cedar (*Thuja occidentalis*). There is little agricultural land, which occurs as primarily pasture and hayfields rather than in cultivated crops. Logging was a major land use during much of the twentieth century, but tourism has increased greatly over the last several decades and is now the major industry. Peek et al. (1976) provide a more detailed description of vegetative conditions and history of this area.

Historically, woodland caribou were more common than moose in the study area (Swanson et al. 1945). Caribou are generally considered to have disappeared as white settlement of the area increased and logging created abundant habitat suitable for white-tailed deer, which quickly populated the area. Throughout this change, moose remained the second most abundant ungulate.

Data collection

The study area was subdivided into 196 whole or partial townships, a square survey unit 9.66 km on each side (Fig. 1). We used data on the occurrence of giant liver flukes in adult (≥ 2 years old) moose collected by individual townships between 1972 and 2000. Data came primarily from hunter-killed moose, and to a lesser extent, moose killed by motor vehicles. Sample sizes varied between 0 and 45 adult moose examined per township over 29 years. We removed three outlying samples with small numbers of moose, and

considered a total sample of 90 townships in our analyses. We assumed that trends we documented were constant over time; sample size was too small to partition data by year.

Direct information on population densities of white-tailed deer was not available. We did have numbers of male deer harvested between 1981 and 2000 by hunters in six hunting zones that spanned our study area. Again, we assumed that trends in harvest were constant over time. We used those harvest rates to index population density of white-tailed deer. Harvest of ungulates can be strongly correlated with their abundance, and provides a good index to population size (Bowyer et al. 1999; Kaji et al. 2010; Boyce et al. 2012), especially for our large sampling units.

Data analysis

We used kriging (Krige 1951) to develop a response surface to predict the occurrence of giant liver flukes in moose across the study area, which we depicted using Playfair’s circles. This method is especially useful for illustrating “aerial” results in two dimensions (Tufté 1983), which included space and magnitude of infection across townships. Kriging is a geospatial technique to interpolate the value of variables at unobserved locations from observations at nearby locations. Kriging can estimate the uncertainty of prediction; many deterministic models cannot do so (Zhong et al. 2005). Kriging, however, requires a number of assumptions (Fortin and Dale 2005; Fortin et al. 2010). First, data must exhibit stationarity; that is, statistical properties must be the same across the entire study area. To test for stationarity, we first fitted various global polynomial models to data on liver flukes in moose. Kriging also requires the estimation of spatial autocorrelation among data from semivariance analysis. Finally, if spatial autocorrelation is present, the magnitude of that parameter must be the same in all directions (isotropy; Fortin and Dale 2005). Our analyses of data closely followed methods recommended by Fortin et al. (2010). We acknowledge that other sophisticated methods exist for analyzing data, such as “data mining” techniques proposed by Hochachka et al. (2007). Those methods, however, are not suitable for hypothesis testing (Hochachka et al. 2007).

We also determined the abundance of suitable habitats for snails, the obligatory intermediate host of giant liver flukes, using the 2001 National Land Cover Database (available at <http://deli.dnr.state.mn.us/>). This database is a raster coverage with 30×30 m cells. The coverage consists of 15 land cover types, two of which were thought to be suitable as habitats for snails. Woody wetlands were defined as areas where forest or shrub-land vegetation accounted for >20 % of vegetative cover, and the soil or substrate was periodically saturated with or covered with water. Emergent herbaceous wetlands were defined as areas where perennial

herbaceous vegetation accounted for >80 % of vegetative cover and the soil or substrate was periodically saturated with or covered with water. We determined the proportion of each township covered by these two wetland types. We did not use the open-water class in the database, because it included deep and fast-flowing waters that were not suitable snail habitat.

To examine the relationship between the occurrence of liver flukes in moose and the index to population density of white-tailed deer and the proportion of wetland habitats, we used ordinary least-squares multiple regression adjusted for the number of independent variables (R^2_{adj}) (Neter et al. 1985). We examined colinearity between independent variables with variance inflation factors (VIF); values of <10 are thought to be free from problems with redundancy in explanatory variables (Neter et al. 1985).

We examined residuals from ordinary least-squares multiple regression for spatial autocorrelation using global Moran's I. Where such autocorrelation was present, we used geographically weighted multiple regression techniques (Fotheringham et al. 2002; Charlton and Fotheringham 2009). We compared the two models using Akaike Information Criterion adjusted for small sample size (AIC_c) (Burnam and Anderson 2002). This method is not prone to over-parameterizing models when only a few variables are considered (Hochachka et al. 2007). All analyses were performed with Arc GIS 9.3 (ESRI, Redlands, California, USA).

Results

The mean (\pm SD) prevalence of giant liver flukes in moose for the 90 townships considered was 17.4 ± 23.2 %. The percent occurrence on wetland habitat across those same townships was 5.2 ± 7.5 %, with a tendency for wetland habitat to decline moving from the southwest to the northeast across our study area (Appendix 2). The density of male white-tailed deer harvested across six hunting zones was 0.71 ± 0.42 deer/km².

A noticeable trend in increasing rates of occurrence of giant liver flukes in moose was evident when moving to the west and southwest across our study area (Fig. 1), which indicated a violation of the assumption of stationarity when conducting kriging. We therefore conducted a trend-surface analysis by fitting a series of global polynomial models. A second-order global polynomial fit better (mean error=0.029, root mean square=16.19, Fig. 2a) than either a first-order (mean error=-0.225, root mean square=19.58) or third-order (mean error=0.060, root mean square=17.95) polynomial. We then de-trended data for liver flukes using that second-order global polynomial model for all subsequent analyses, thereby meeting the assumption of stationarity.

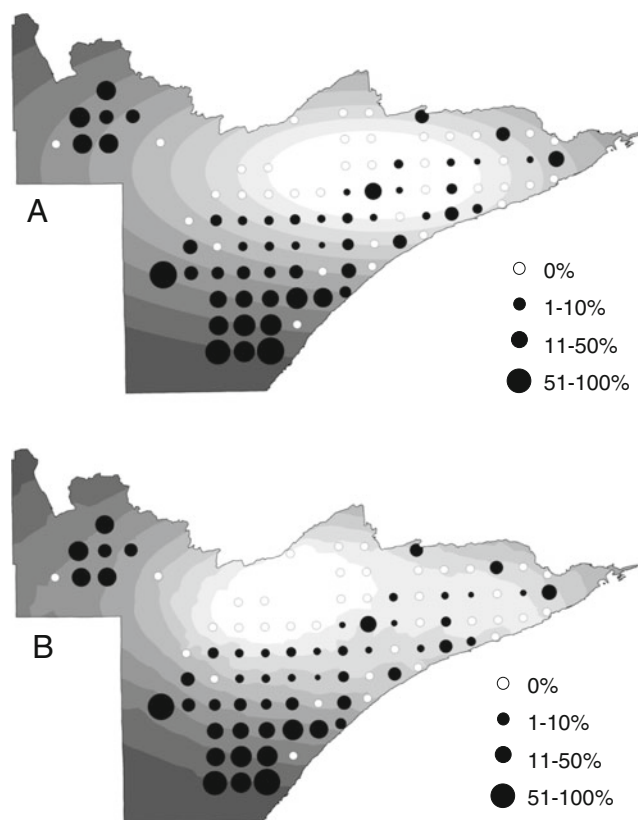


Fig. 2 **a** Second-order global polynomial model for infection rates of giant liver flukes in moose in northeastern Minnesota, USA and **b** kriged response surface based on de-trended data using a circular semivariogram model. Note shift of lowest estimated infection rates to the west with additional information from kriging

We determined that a circular semivariogram (range=130 km) was an appropriate model by examining the pattern of spatial autocorrelation in our data using semivariance analysis. Spatial autocorrelation did not differ as a function of direction (anisotropy), thereby meeting the assumption of isotropy. Finally, we used kriging to arrive at a predicted response surface for the occurrence of giant liver flukes among moose across our study area (Fig. 2b). By bringing stochastic information to bear in the kriged model, we shifted the zone of lowest predicted occurrence slightly westward compared with the deterministic global polynomial model. The kriged model appeared to better fit the pattern observed in raw data (Fig. 2a, b). This disease map provides an estimate of relative risk for adult moose becoming infected with giant liver flukes.

Occurrence data for liver flukes in moose indicated a strong relationship with the index of population density of white-tailed deer based on rates of harvest (Fig. 3a). Correlational analyses indicated that the occurrence of liver flukes in moose was influenced more by the density of white-tailed deer based on rates of hunter harvest ($r=0.54$) than was the proportion of wetland habitats ($r=0.25$). Ordinary least-squares multiple regression ($R^2_{adj}=0.29$, $AIC_c=795.3$)

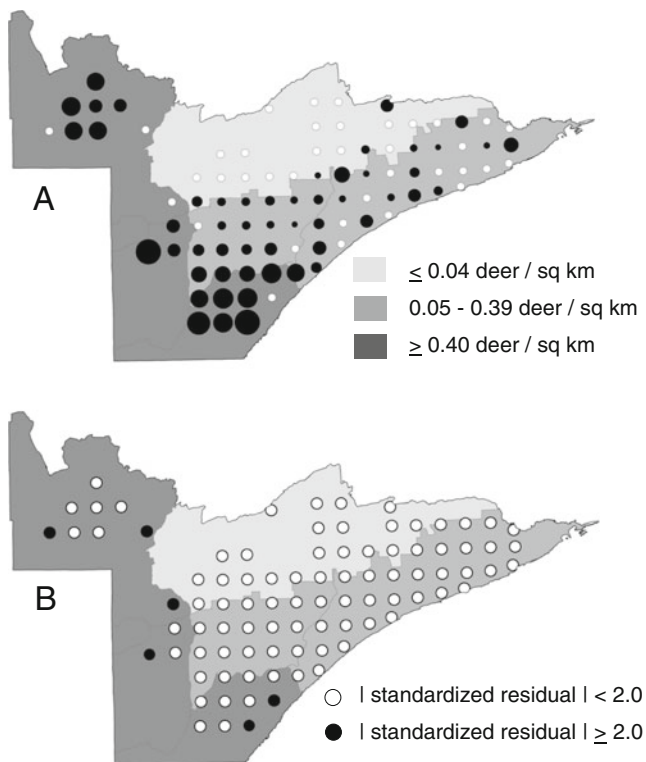


Fig. 3 **a** Infection rate of giant liver flukes related to annual hunter harvest rates of white-tailed deer by hunting zone, northeastern Minnesota, USA. **b** Absolute values of standardized residuals from geographically weighted regression analysis indicating good model fit in most areas except in six townships at the western extent of data

documented a strong relationship between the occurrence of liver flukes in moose and population density of white-tailed deer ($p < 0.001$), but a weaker relationship for wetland habitats ($p = 0.16$). Residuals from that analysis, however, were spatially correlated (global Moran's $I = 0.287$, $P < 0.01$). A geographically weighted multiple regression produced a stronger relationship ($R_{ad} = 0.60$, $AIC_c = 765.7$). There was no indication of problems with collinearity in our analysis ($VIF = 1$). Mapping the absolute values of the standardized residuals from the geographically weighted regression indicated good model fit in all areas except for six townships at the western extent of our data (Fig. 3b).

Discussion

We demonstrated a strong geospatial pattern in the prevalence of giant liver flukes in moose in northeastern Minnesota. That pattern likely reflected the density of white-tailed deer, which are a normal definitive host for the giant liver fluke, and are involved in spreading this infection to moose via snails. Suitable wetland environments necessary to support this intermediate host of the parasite also must be related to the prevalence of liver flukes in moose. Adding

the proportion of wetland habit by township, however, brought no further information to the model, but slightly lowered the regression coefficient as a result of the penalty to the adjusted R^2 of adding a second explanatory variable. Large areas of wetland habitat were absent from our study area, although small areas showed spatial variability in abundance among townships. Larger areas of wetland habitat did increase in abundance to the west and southwest but not within the westernmost extent of our study area. Within the area for which we examined data, the presumed density of white-tailed deer was a far better variable explaining the occurrence of liver flukes in moose than was variability in suitable wetland habitats for snails. This outcome likely occurred because both infected white-tailed deer (a definitive host for this parasite) and suitable snail habitat must be present for moose to become infected.

One final factor that might affect the prevalence of liver flukes in moose is the abundance of moose. Such an effect might result from a bias related to number of moose available to sample; sufficiently low densities of moose might cause an underestimation of prevalence. Only the density of white-tailed deer, however, strongly predicted the geospatial distribution of moose parasitized by giant liver flukes. Moreover, a density-dependent response in prevalence of liver flukes is not expected, because of a relatively low prevalence of infection, and more importantly, because moose are a dead-end host and not involved in infecting deer or other moose.

We assumed that the harvest of white-tailed deer indexed the abundance of these large herbivores. There are several articles relating harvest to density of ungulates (Bowyer et al. 1999; Kaji et al. 2010; Boyce et al. 2012). This line of reasoning also is supported by the strong relationship between harvest of white-tailed deer and the prevalence of giant liver flukes in moose.

Our research was not designed to test whether the giant liver fluke was capable of causing mortality in moose that might precipitate a decline in the population in northwestern Minnesota (sensu Murray et al. 2006). Prevalence of liver flukes was much higher in northwestern (89 %) compared with northeastern Minnesota (17.4 %), but our result does not demonstrate a causal link between infection with liver flukes and the decline in the moose population in the northwest. We contend, that determining the spatial distribution of moose infected with liver flukes on the landscape, and factors that influence rates of infection, are nonetheless important steps in better understanding effects of giant liver flukes on populations of moose.

Knowledge of spatial relationships is essential to understanding when parasites might become agents of disease and cause substantial mortality in host populations. This includes, for example, sorting effects of parasitism from density-dependent mechanisms in the dynamics of moose

populations. Such an outcome is not dependent upon population density per se, but upon density of large herbivores in relation to the carrying capacity (K) of the habitat (sensu Kie et al. 2003). Populations at or near K experience intense intraspecific competition, which results in poor physical condition, reduced immuno-competence, and potentially high rates of infection by parasites (Eve and Kellogg 1977; Sams et al. 1996). Moreover, such populations are likely to experience mostly compensatory mortality, which is unlikely to result in population reductions (Kie et al. 2003; Pierce et al. 2012). Determining whether poor physical condition leads to an increased rate of infection or the rate of increased infection causes poor physical condition is a critical element in determining whether parasites are likely to regulate moose populations. Our research indicates that a spatial component also should be considered in such studies, especially where other variables, such as density of white-tailed deer and percent of wetland habitat for snails can play critical roles in determining prevalence of infection for moose.

Most studies of disease mapping involve human pathogens (Carrat and Valleron 1992; Kleinschmidt et al. 2000; Zhong et al. 2005; and many others). Disease maps for large, free-ranging mammals are rare. We applied a robust kriging approach to better understand the occurrence of giant liver flukes in moose across a broad geographical extent. This method allowed us to estimate the prevalence of infection for moose for areas for which no data existed by using data from adjacent areas. We also produced a risk map for occurrence of infection of moose by liver flukes. Density of white-tailed deer likewise exhibited a strong geospatial pattern, which allowed us to model infection of moose by flukes, and more fully comprehend the role of deer in this process. We suggest that a landscape approach that includes spatial components will become a powerful tool for investigating and monitoring host–parasite relationships. We further assert that our geospatial approach will be useful in understanding other diseases of wildlife.

Conclusions

1. We demonstrated a strong geospatial pattern in the occurrence of giant liver flukes in moose in northeastern Minnesota, USA, moving from the northeast to the west and southwest across our study area.
2. We used kriging to develop a predictive response surface of relative risk for moose becoming infected by giant liver flukes.
3. Ordinary least-squares multiple-regression revealed that the density of white-tailed deer was more strongly related to the occurrence of liver flukes in moose than was

the proportion of wetland habitats, but spatial autocorrelation was present.

4. Geographically weighted multiple regression indicated that liver flukes in moose were best predicted by an index to the density of white-tailed deer, a definitive host of this parasite.
5. Our landscape approach, including spatial components summarized as disease maps, should be useful in understanding host–parasite relationships in other wildlife.

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