Local spatial modeling of white-tailed deer distribution

Haijin Shi [a,*], Edward J. Laurent [a], Joseph LeBouton [b], Laila Racevskis [c],
Kimberly R. Hall [a], Michael Donovan [d], Robert V. Doepker [e],
Michael B. Walters [b], Frank Lupi [a,c], Jianguo Liu [a]

[a] *Center for Systems Integration and Sustainability, Department of Fisheries and Wildlife, 13 Natural Resources Building,
Michigan State University, East Lansing, MI 48824, USA*
[b] *Department of Forestry, 126 Natural Resources Building, Michigan State University, East Lansing, MI 48824, USA*
[c] *Department of Agricultural Economics, 213 Agriculture Hall, Michigan State University, East Lansing, MI 48824, USA*
[d] *Michigan Department of Natural Resources, Stephens T. Mason Building, Lansing, MI 48909, USA*
[e] *Michigan Department of Natural Resources, Norway, MI 49884, USA*

Abstract

Complex spatial heterogeneity of ecological systems is difficult to capture and interpret using global models alone. For this reason, recent attention has been paid to local spatial modeling techniques. We used one local modeling approach, geographically weighted regression (GWR), to investigate the effects of local spatial heterogeneity on multivariate relationships of white-tailed deer distribution using land cover patch metrics and climate factors. The results of these analyses quantify differences in the contributions of model parameters to estimates of deer density over space. A GWR model with local kernel bandwidth was compared to a GWR model with global kernel bandwidth and an ordinary least-squares regression (OLS) model with the same parameters to evaluate their relative abilities in modeling deer distributions. The results indicated that the GWR models predicted deer density better than the traditional ordinary least-squares model and also provided useful information regarding local environmental processes affecting deer distribution. GWR model comparisons showed that the local kernel bandwidth GWR model was more realistic than the global kernel bandwidth GWR model, as the latter exaggerated local spatial variation. The parameter estimates and model statistics (e.g., model R^2) of the GWR models were mapped using geographic information systems (GIS) to illustrate local spatial variation in the regression relationship and to identify causes of large-scale model misspecifications and low estimation efficiencies.
© 2005 Elsevier B.V. All rights reserved.

Keywords: Geographically weighted regression; Ordinary linear-squares regression; White-tailed deer; Spatial heterogeneity; Climate; Patch metrics; Landscape metrics; Geographic information systems

* Corresponding author. Tel.: +1 517 432 8256; fax: +1 517 432 1699.
  E-mail address: hshi@msu.edu (H. Shi).

1. Introduction

Understanding spatial distribution patterns of wildlife, such as white-tailed deer (*Odocoileus virginianus*), is a critical step toward identifying key relationships between wildlife and their impacts (e.g., browsing, bark stripping) on natural resources (McShea et al., 1997; Liu and Taylor, 2002). However, difficulties in assessing wildlife distribution make wildlife management complicated, especially in forested areas (Radeloff et al., 1999). In order to predict wildlife distribution patterns accurately, various modeling methods have been employed to take advantage of mapped vegetation associations (e.g., land cover). Techniques used for these modeling efforts include regression trees (Stankovski et al., 1998), poisson regression (White et al., 2004), logistic multiple regression (Pearce, 1987; Augustin et al., 1996), and linear multiple regression (Radeloff et al., 1999). However, the primary means of wildlife distribution modeling is ordinary least-squares regression (OLS; Coppolillo, 2000; Buckland et al., 2001). The two general assumptions of OLS are that observations are independent and variance is homogeneous among samples.

Unfortunately, the assumptions of independence and constant variance of OLS are often violated due to spatial effects on variables sampled across a landscape (Gribko et al., 1999). Spatial effects consist of spatial autocorrelation (i.e., spatial dependency) and spatial heterogeneity (i.e., spatial nonstationarity) (Anselin, 1988; Anselin and Griffith, 1988). Spatial autocorrelation is defined as a situation in which one variable is spatially related to the same variable located nearby. Tobler's law of geography gives a more direct interpretation: "Everything is related to everything, but near things are more related than distant things" (Anselin, 1988). When spatial autocorrelation exists in the error terms of a regression model, it biases the estimation of error variance (Shi and Zhang, 2003). However, regression coefficients remain unbiased. Thus, spatial autocorrelation elicits misleading significance tests and measures of model fit (Anselin and Griffith, 1988). Spatial heterogeneity, on the other hand, is defined as "the complexity and variability of a system property in space" (Li and Reynolds, 1994, p. 2446). Spatial heterogeneity, therefore, explains systematic changes in the contribution of different model parameters or responses of predicted variables over space (Anselin

and Griffith, 1988; Anselin, 1990). It is related to locations in space, missing variables, and functional misspecification (Anselin, 1988; Fotheringham, 1997). If spatial heterogeneity is not considered in regression models, it will result in biased parameter estimates, misleading significance tests, and suboptimal prediction (Anselin and Griffith, 1988).

Recently, a simple but powerful method called Geographically weighted regression (GWR) has been proposed for exploring spatial heterogeneity (Brunsdon et al., 1996; Fotheringham et al., 2000, 2002). GWR is an extension of the traditional regression framework (Zhang and Shi, 2004), and operates by estimating local rather than global parameters at each point on a landscape. Hence, GWR explicitly incorporates the spatial locations of data, and therefore, can be used to investigate the influence of spatial heterogeneity on model fit. The local estimation of model parameters is derived by weighting all neighboring observations using a decreasing function of distance. In this way, the impacts of the neighbors nearby are stronger than those farther away. Additionally, a threshold, called the kernel bandwidth, is specified to indicate the distance beyond which neighbors no longer have influence on local estimates.

As originally presented, the GWR method used a global kernel bandwidth, which means the kernel bandwidth was constant across locations (Brunsdon et al., 1996; Fotheringham et al., 2000, 2002). Recently, another approach was proposed by Pàez et al. (2002a) to choose different local kernel bandwidths at different locations. Given that most landscapes are characterized by spatial heterogeneity, it is probable that local estimation of parameters is more realistic than global estimation.

There are several advantages of GWR over other available methods of spatial prediction. In addition to performance measures (e.g., goodness-of-fit, *t*-values) of traditional regression methods, GWR produces a set of parameter estimates and R^2 values at each sampled point. By mapping these parameter estimates and model statistics using visualization tools (e.g., GIS), local spatial variation in the regression relationships can be investigated (e.g., Brunsdon et al., 1996; Fotheringham and Brunsdon, 1999; Fotheringham et al., 2000; Pàez et al., 2002a). GWR, therefore, provides a useful tool for ecologists to explore wildlife-habitat associations and how they vary spatially across a land-

scape. This technique also provides opportunities for ecologists to identify causes of large-scale model mis-specifications and low estimation efficiencies.

In this paper, we provide an overview of the GWR methodology for modeling spatial heterogeneity of ecological data using the spatial distribution of white-tailed deer as a case study. We began with a linear regression model developed to predict deer density as a function of landscape structure defined by land cover and climate. Our goal was to model the relationship between deer density and landscape descriptions over areas of use. The quantified relationship was desired to identify ways of moderating browsing pressure on vegetation regeneration via strategic modifications to deer density and habitat. To compare spatial model-ing approaches, we fit the linear regression model with OLS and two different GWR methods (i.e., local kernel bandwidth and global kernel bandwidth). We compared the results by testing model fit for the three methods using typical performance measures (e.g., goodness-

of-fit), and through mapping parameter estimates used to predict white-tailed deer distribution.

2. Methods

2.1. Study area

Our study area included eight counties (i.e., Baraga, Dickinson, Gogebic, Houghton, Iron, Keweenaw, Menominee and Ontongaon) in Michigan's Upper Peninsula (UP) (Fig. 1). The 2345 km^2 area is charac-terized by a spatial mosaic of forest stands that include northern hardwood (sugar maple, American beech, white ash, yellow birch, basswood), wetland hard-wood/conifer (black ash, red maple), and aspen/birch among others. These eight counties were chosen because they are dominated by forests and historical data indicates high spatial variation in deer density over the area (Doepker et al., 1994). This heterogeneous dis-
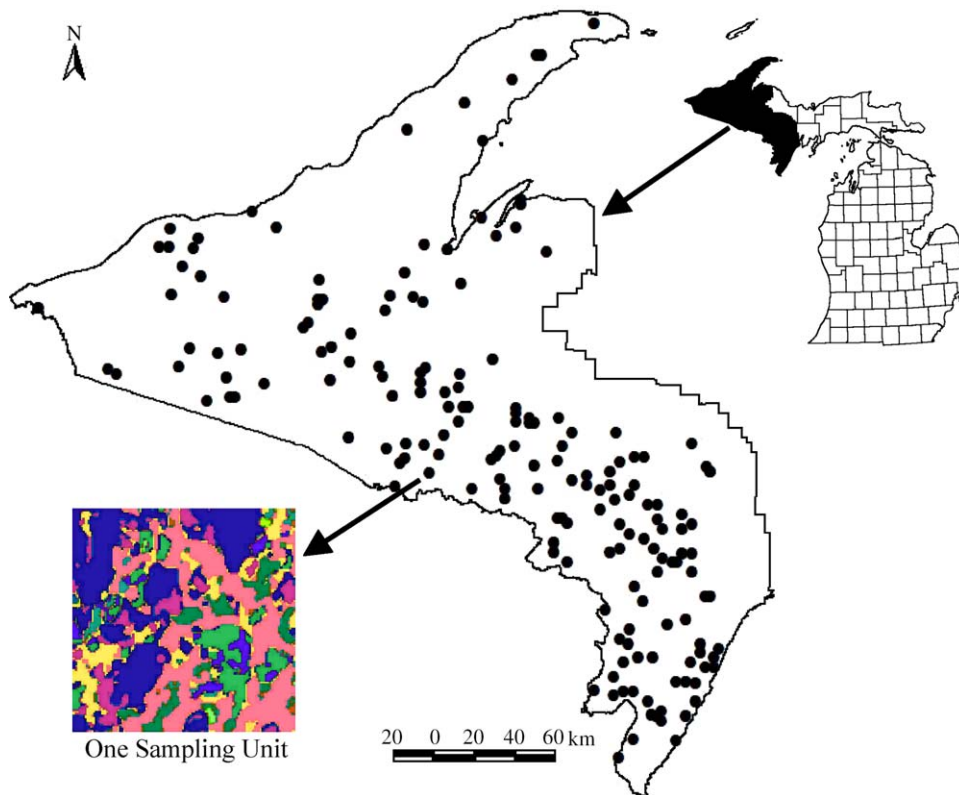

Fig. 1. Map of the study area in the Upper Peninsula, Michigan (each dot indicates a township section sampled for deer pellet groups).

tribution implies that different ecological factors (e.g., local climate, forest type) influence deer density (e.g., Nelson and Mech, 1981; Kirchhoff and Schoen, 1987).

2.2. Deer density

We used surveys for deer pellet groups to estimate relative deer density in winter. Deer pellet count data used in this study were collected in the spring of 1991 by members of the Michigan Department of Natural Resources (MDNR). Prior to data collection, the region was classified into three strata of deer abundance, which were sampled as separate entities. The region was further divided into township sections of 1069 m × 1069 m or 2.59 km^2 (1 square mile). The number of sample township sections sampled within each stratum was based upon its area and the variability of pellet density observed in previous years (Hill, 1999). Due to land survey corrections and the irregular shape of lakeshores, some sections may contain less than 2.59 km^2 of land area, but the township section was considered the smallest spatial unit for these analyses.

Specific sections identified for sampling were selected randomly within strata so that each section within a stratum had the same probability of being chosen. Within each selected township section, a series of five 80.54 m^2 (1/50-acre) rectangular plots were randomly located and surveyed for groups of deer pellets. These five samples were not georeferenced within sections and thus only provided a statistical distribution of deer density for the section. The average number of pellet groups counted among the five plots was multiplied by 32,000 to estimate the average number of pellet groups within each township section (2.59 km^2).

To use pellet count data to estimate deer density, two types of ancillary data were needed: the rate that pellet groups were produced and the time period over which they were deposited. The assumed pellet deposition rate for the UP was 13.4 times per deer in a 24-h period (Hill, 1999). In our study area, the time period over which all pellet groups had been deposited was defined as beginning after leaf fall in the previous autumn and ending on the average date of pellet surveys. We chose to define the time period in this way because fallen leaves form a mat that hides groups dropped earlier in the year. Hence, only those groups dropped after leaf fall are visible. However, biologists were trained to dis-

tinguish new pellet groups from the old in areas where leaf cover was sparse (Hill, 1999). For our data set, this period of pellet deposition was assumed to be 187 days. Thus:

Estimated deer density (per section)

$$= \frac{\text{average pellet groups} \times 32,000}{187 \times 13.4} \quad (1)$$

2.3. Ecological variables

The primary limiting factors affecting winter deer density in the study area include hunting, food availability, winter cover and climate (Xie et al., 1999). Because no spatially compatible estimates of hunting effort were available for this area, we excluded hunting from these analyses. Increased snow depth and decreased temperatures increase the mortality of deer in the UP as a function of increased energy demands (Ozoga and Gysel, 1972; Nelson and Mech, 1981; Doepker et al., 1994). Thus, we used local estimates of average snow depth and minimum temperature as predictor variables in our regression model. Climate statistics were 30-year averages (1971–2000) calculated between November 1st and April 30th (ZedX Inc., http://www.zedxinc.com/, 1 km × 1 km resolution). This period covers 181 days, similar to the period of pellet data used in this study (187 days).

High resolution estimates of average snow depth and minimum temperature in each monthly database were generated by applying a mathematical algorithm to the 30-year (1971–2000) climatological station records (National Climatic Data Center, http://www.ncdc.noaa.gov/oa/ncdc.html). These estimates were compared to climate station data collected in 1991 (http://www.ncdc.noaa.gov/oa/ncdc.html). A *t*-test indicated the absence of significant differences for average snow depth and the minimum temperature between the 30-year averages and 1991 samples (*p*-value < 0.05). In order to make our model more representative, we used the interpolated 30-year averages of snow depth and minimum temperature in our regression model.

Deer respond to wintertime conditions by concentrating in deeryards. In the UP, deeryards are typically white cedar swamps. These areas provide refuge from heavy snow, high winds, and radiant heat loss (Blouch, 1984). In mild winters or where cedar swamps are lack-

ing, mixed conifer or mixed hardwood/conifer can also serve as deeryards (Blouch, 1984). While dense conifer forests provide winter cover for deer, nearby hardwood stands can provide browse for deer to maintain fat stores over winter (Blouch, 1984). Fatter deer are capable of enduring harsher winter conditions (Ozoga and Gysel, 1972).

To include data describing the spatial distribution of potential deeryards and hardwood stands in our model, we used a land cover map available in grid format from the state of Michigan (http://www.mcgi.state.mi.us/). This map was derived from 1991 Landsat 5 TM imagery consisting of $30\,m \times 30\,m$ pixels having 27 landcover classes with a published accuracy of 90.2% (http://www.mcgi.state.mi.us/). Forest cover in the eight study counties was 84.4%. Of that portion, northern hardwood and wetland hardwood/conifer forest accounted for 62.7% and the other 37.3% was composed of mixed conifer, white cedar, mixed pine, jack pine, hemlock, etc. The remaining non-forest cover was shrubland, residential, agricultural, bare land and water.

Landcover maps were resampled to standardize the number of landcover pixels per section used in the following analyses. We resampled the landcover map to a pixel size of $40.225\,m \times 40.225\,m$ using ArcView 3.2 (Environmental Systems Research Institute Inc.). Therefore, each section ($1069\,m \times 1069\,m$) consisted of exactly the same number of $40.225\,m$ pixels ($40\,pixels \times 40\,pixels$). Pixel values in the resampled image were interpolated from nearest neighbors in the original map. While resampling the image to a larger pixel size likely resulted in a loss of some small patches (Kimerling, 2002) and a reduction in the perimeter to area ratio of patches that were maintained, we assumed that this smoothing of fine scale data to $0.0016\,km^2$ pixels would not reduce the predictive accuracy of relatively coarse ($2.59\,km^2$) spatial trend estimates of deer density.

In winter, the maximum home range of white-tailed deer in the UP is about $18.6\,km^2$ (7.2 square mile; VanDeelen et al., 1998). Because this home range is larger than a township section, the vegetation characteristics of areas surrounding sampled sections (e.g., the context sections) should be taken into account. If such contextual effects were not considered, significant biases could be introduced into spatial analyses (Mazerolle and Villard, 1999; Wiens, 2001).

Three methods are available for contextual correction: (1) establishing a buffer zone (Sterner et al., 1986), (2) using a toroidal edge correction (Ripley, 1979, 1981), and (3) using an edge correction by weighting (Getis and Franklin, 1987; Andersen, 1992). The second method is used when there is no neighboring information available. The third method is not suitable for this study because of the complexity of patch metrics (see below). In this study, the easiest and most practical way for contextual correction is to use a buffer zone. Each sampled township section ($1 \times 1\,mile = 1.6 \times 1.6\,km$) was, therefore, extended along all edges by an additional section. Consequentially, the sampled section and its eight neighboring sections composed one sampling unit for subsequent analyses. The resulting sampling unit (3×3 sections $= 23\,km^2$) provides an area large enough to represent deer habitat features relative to the average deer's winter home range of $18.6\,km^2$ (VanDeelen et al., 1998).

Within each sampling unit (nine township sections), we calculated several landscape indices for each landcover class. We chose these indices based on knowledge of deer life history traits. Deer prefer to forage along forest edges (e.g., Kie et al., 2002), therefore, landscape features such as the length of edges and the variation in patch area within a sampled section were considered important determinants of deer distribution. Specific patch features (e.g., patch size) and their spatial arrangement also affect deer density (Bowyer et al., 2002). For these reasons, we calculated the area, number of patches, mean patch size, patch size coefficient of variance, patch size standard deviation, total edge, edge density, average patch perimeter-area ratio, mean shape index, and area weighted mean shape index for each landcover class within each sampling unit using Patch Analyst 3.1 (Rempel and Carr, 2003). These patch metrics, along with the climate variables described above were the predictor variables assessed in our model development.

As mentioned above, the range of deer is generally much broader than one township section (Verme, 1973; VanDeelen et al., 1998; Lovallo and Tzilkowski, 2003). As a result, the deer density per section might not represent a realistic estimate of deer density among sections. In order to obtain the deer density per sampling unit (3×3 sections), deer density from sampled sections was kriged across the study area using an exponential
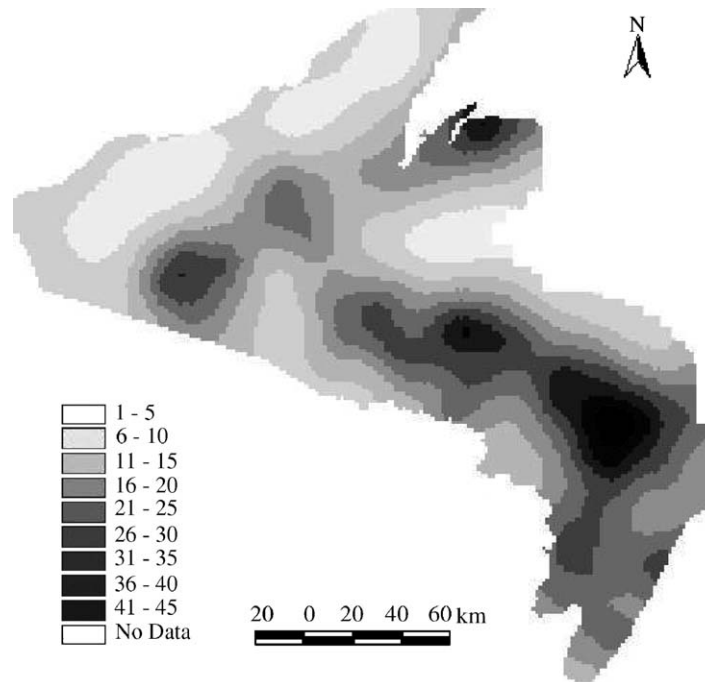
Fig. 2. Estimated deer density (number of deer/km^2) during 1991 in the Upper Peninsula, MI.

variogram model (S-plus 6.2, Insightful Corporation) manually fitted with Range = 35,000 m, Nugget = 45, Sill = 550. We used the resulting kriged deer density for each sampling unit (Fig. 2) as the dependent variable in the following deer distribution models.

2.4. Modeling techniques

We employed several statistical techniques to develop the winter white-tailed deer distribution model. First, we used correlation analysis and stepwise regression to remove unimportant and redundant predictor variables. Second, we fit the OLS and global and local kernel bandwidth GWR models using the remaining variables as predictor variables and the kriged deer density as dependent variable. Third, we evaluated the OLS model fit through residual analysis and the Shapiro-Wilk test. Fourth, we compared the difference between local and global kernel bandwidth GWR models with their kernel bandwidth and the parameter estimates. Fifth, we tested local nonstationary using the parameter variation test and the locational heterogeneity test. Finally, we evaluated the improvement of GWR over

OLS using goodness-of-fit test and the Lagrange Multiplier (LM) test.

2.4.1. Correlation analysis and stepwise regression

Before performing correlation analysis and stepwise regression, we used a log transform to normalize skewed dependent and predictor variables. Correlation analysis was employed to reduce the number of predictor variables and to ensure independence of predictor variables used later in linear regression models. We kept predictor variables for further analysis only if Pearson correlation coefficients with deer density were greater than +0.15 or less than −0.15. Also, if correlation coefficients between predictor variables exceeded 0.65, we removed redundant variables (i.e., lower Pearson correlation coefficient with deer density).

We used backward stepwise regression to remove non-significant predictor variables after the correlation analysis. Using this approach, we kept all predictor variables in the model at the beginning of the stepwise regression. During each step of this analysis, we removed one predictor variable, if its significance level

was greater than 0.15. We chose the significance level of 0.15, because the traditional alpha level of 0.05 is inadequate when building stepwise regression models. It often excludes important variables from the final equation (Hosmer and Lemeshow, 1989). We repeated the process until all the remaining predictor variables were statistically significant.

2.4.2. Ordinary least squares regression analysis

The following linear regression model was used:

$$y_i = \beta_0 + \sum_{j=1}^{p} X_{ij}\beta_j + \varepsilon_i \qquad (2)$$

where β_0, β_1, ..., β_p are parameters; ε_1, ε_2, ..., ε_n are random error terms whose distribution are $N(0, \sigma^2 I)$ assuming constant variance, with I denoting an identity matrix. y_i is the dependent variable and X_{ij}, the independent variable ($i = 1, 2, ..., n$ and $j = 1, 2, ..., p$). In this model, with the assumption of independent observations and constant variance, we obtained the OLS estimate of β_i as

$$\hat{\beta}_i = (X^T X)^{-1} X^T y \qquad (3)$$

where superscript T denotes the transpose of a matrix. After the estimation, we interpreted the model statistics (e.g., parameter estimates, R^2) statistically and ecologically.

2.4.3. Local modeling and analysis using GWR model

2.4.3.1. Model fitting. Among other differences, OLS and GWR differ in that the latter uses a weight matrix in the estimation procedure (Brunsdon et al., 1996, 1998; Pàez et al., 2002a). Assume the weight matrix is:

$$W_i(u_i, v_i) = \begin{pmatrix} w_{i1} & 0 & \cdots & 0 \\ 0 & w_{i2} & \cdots & 0 \\ \vdots & \vdots & w_{ij} & \vdots \\ 0 & 0 & \cdots & w_{in} \end{pmatrix} \qquad (4)$$

where (u_i, v_i) are the coordinates of location i. Then the estimator of β_i given by GWR is:

$$\hat{\beta}_i = (X^T W_i(u_i, \ v_i) X)^{-1} X^T W_i(u_i, \ v_i) y \qquad (5)$$

In general, the weighting function, called the kernel function, is taken as the exponential distance-decay form:

$$w_{ij} = \exp(-\tau d_{ij}^2). \qquad (6)$$

where d_{ij} is the distance between the subject i and its neighboring observation j and τ, the kernel bandwidth.

A GWR model can use either a global kernel bandwidth (i.e., a constant over space) or local kernel bandwidths (i.e., the threshold varies spatially). A global kernel bandwidth can be obtained in three ways: (1) a predefined bandwidth based on existing knowledge, (2) a cross-validation procedure, or (3) a method that minimizes the Akaike Information Criterion (AIC) for fitting the regression model (Brunsdon et al., 1998; Fotheringham et al., 2000, 2002). There are some limitations in using these methods of kernel bandwidth estimation. Although the use of a predefined bandwidth makes computation simpler, its utility depends on the researchers' experience and ability to choose the "best" subjective bandwidth. The cross-validation procedure is an objective approach, however, a reasonable global kernel bandwidth is sometimes computationally impossible (Pàez et al., 2002a). Also, the cross-validation and AIC methods in GWR are time consuming when applied to large number of samples.

Although there were some limitations in the cross-validation and AIC methods, they were still applicable for our data. Generally, there is no significant difference between the kernel bandwidths obtained from these two methods (Fotheringham et al., 1998, 2002). The cross-validation procedure was, therefore, used to obtain the global kernel bandwidth using a computer software program called GWR 2.0. Detailed information on the software is available at the web site http://www.ncl.ac.uk/geps/research/geography/gwr/.

In order to obtain local kernel bandwidths, Pàez et al. (2002a) proposed a method by assuming that local nonstationarity resulted from nonconstance of variances among the observations. Using this approach, the spatial weights are modified in the GWR regression depending on the variation of local kernel bandwidths. Specifically, the local kernel bandwidth is estimated using the maximum likelihood method (for details, consult Pàez et al., 2002a), allowing the kernel bandwidth to vary over space. This method was shown to provide results with greater accuracy than the global kernel bandwidth (Brunsdon et al., 1996; Fotheringham et al., 2000, 2002). We computed the local kernel band-

widths for each sampling unit using a Matlab (The MathWorks Inc.) extension developed by Pàez et al. (2002a,b). In the local regression analyses, we fitted Eq. (2) to the deer pellet count data by GWR methods with the global and local kernel bandwidth.

2.4.3.2. Comparison between local and global GWR models. The goal of comparing GWR models was to identify whether the local or global kernel bandwidth GWR model could more accurately predict white-tailed deer distribution. The major differences between these two models were the parameter estimates and the kernel bandwidth. We first conducted a comparison between the range of the kernel bandwidth and the rate of decay in the weighting function for measuring the performance of these GWR models. Second, we compared variations of localized parameter estimates quantitatively. Finally, we explored dissimilarity between these two models visually, using contour plots created with ArcView 3.2 (Environmental Systems Research Institute Inc.).

2.4.3.3. Local nonstationarity test. The objective of the test for local nonstationarity was to determine if parameter estimates in the GWR model were significantly different across the study area (Brunsdon et al., 1996; Leung et al., 2000). Even though localized parameter estimates may vary over space, this variation may not be significant. If estimates are not significantly different, then the GWR model is the same as the OLS model. There are three ways to make this test: (1) the Monte Carlo test (Brunsdon et al., 1996), (2) the parameter variation test (Leung et al., 2000), and (3) the locational heterogeneity test (Pàez et al., 2002a). The parameter variation test is based on the Monte Carlo approach proposed by Brunsdon et al. (1996) and approximates an *F*-test (for detailed information, see Leung et al., 2000). These two tests are developed to test local nonstationarity for the global kernel bandwidth GWR model and are available with GWR 2.0. In this study, we used the parameter variation test. The locational heterogeneity test is developed specifically for the local kernel bandwidth GWR model. This test is based on the Bonferroni probability inequality, which is the inference for simultaneously testing a certain number of hypotheses. This test is a *t*-test with degree of freedom $n–p$, where n is the number of observations and p is the number of parameters in the GWR model.

We tested local nonstationarity of parameter estimates in the local kernel bandwidth GWR model using Pàez et al. (2002a,b) Matlab extension.

2.4.3.4. Goodness-of-fit test. Given the greater flexibility of the GWR coefficients over space, GWR always provides a better model fit in terms of the residual sum of squares (Brunsdon et al., 1996; Fotheringham et al., 2002). However, it is important to test whether the GWR models offer a statistically significant improvement over the OLS model. Brunsdon et al. (1996) and Leung et al. (2000) proposed approximate *F*-tests to test whether there is an improvement of GWR with a global kernel bandwidth over OLS. We performed this test using the computer software program, GWR 2.0.

For the local kernel bandwidth GWR model, the improvement over OLS was tested using the Lagrange Multiplier test (Breusch and Pagan, 1979, 1980; Pàez et al., 2002a), which is different from the above *F*-tests. The null hypothesis of the LM test is whether the local kernel bandwidth is significantly different from 0 at each sampling unit. If there is no significant difference between the OLS model and the GWR model at that location, then the null hypothesis is not rejected. The LM test is available with Pàez et al. (2002a,b) Matlab extension.

3. Results

3.1. Linear regression analysis

After correlation analysis and stepwise regression, six predictor variables remained in the linear regression model. They were snow depth (SD), patch area of white cedar canopy cover >70% (CA), patch area of mixed pine (MA), northern hardwood patch size coefficient of variance (HV), wetland hardwood/conifer patch size coefficient of variance (WV), and average perimeter-area ratio (PA).

Because the deer pellet count data were collected using stratified sampling (three regional deer density strata), we considered two dummy variables in the linear regression model to account for the difference created by the stratification. The regression analysis indicated that the *p*-values of the two dummy variables were greater than 0.05. For this reason, we did not consider them in the model. Therefore, the final linear regression model was fitted with the OLS method
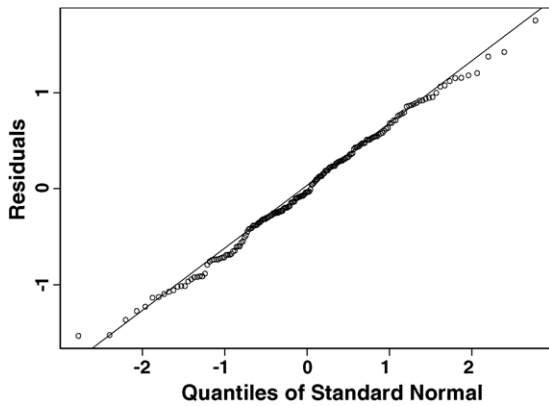
Fig. 3. Quantile-quantile normal plot of the OLS model residual.

as follows:

$$\log(DD) = \underset{(0.7549)}{0.1922} + \underset{(0.0011)}{0.0011HV} + \underset{(<0.0001)}{0.0039WV}$$

$$+ \underset{(0.0070)}{0.0032MA} + \underset{(0.0008)}{0.0416CA}$$

$$+ \underset{(0.0719)}{0.1391\log(PA)} - \underset{(0.0461)}{0.0203SD} \qquad (7)$$

where DD: deer density, log is the natural logarithm, and values in the parentheses are *p*-values. This linear regression model fit moderately well. The multiple R^2 was 0.4038 with *p*-value <0.0001. The intercept and the average perimeter-area ratio were not significant at the significance level of $\alpha = 0.05$. All other predictor variables were significant.

Model fit was further supported through an analysis of residuals. A quantile-quantile plot of the residuals was almost a straight line (Fig. 3) and the Shapiro-Wilk test did not reject the normality of the residual distribution ($W = 0.9947$, *p*-value = 0.7657). Therefore, the linear model described the deer pellet count data well. However, the shape of the residual plot was close to triangular (Fig. 4), indicating the presence of unequal variance (heteroscedasticity) (Hair et al., 1995, p. 113). One remedy to this problem is to use weights in the estimation of parameter values in the OLS model. As mentioned above, GWR is one method of determining the weights for OLS using spatial information.

3.2. GWR kernel bandwidth

For the global kernel bandwidth GWR model, cross-validation estimated a global kernel bandwidth of
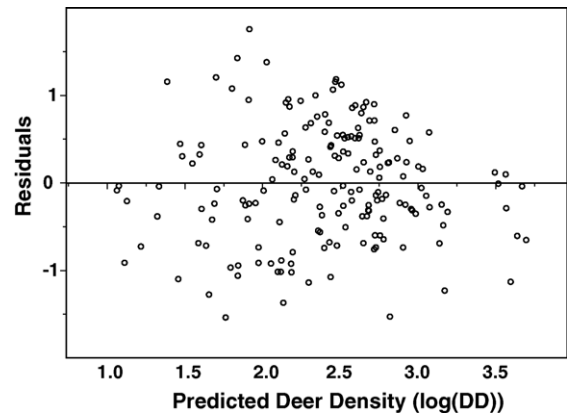

Fig. 4. Residual plot of the observed deer density and the predicted deer density with the OLS model (DD: deer density).

2.2446. For the local kernel bandwidth GWR model, we used all 181 locations to obtain τ for each sampling unit using the maximum likelihood method (Fig. 5; Pàez et al., 2002a).

3.3. Comparison between local and global kernel bandwidth GWR models

The kernel bandwidths and the parameter estimates indicate that differences exist between local and global kernel bandwidth GWR models (Fig. 5 and Table 1). The range of local kernel bandwidths (τ) was 0.0032–0.5366 (Table 1). The maximum of τ (0.5366) from the local kernel bandwidth GWR model was far smaller than the global kernel bandwidth (2.2446).

The range of parameter estimates from the global kernel bandwidth GWR model was much wider than that from the local kernel bandwidth GWR model (Table 1). The GWR model produced localized estimates of the seven model coefficients (β_0, β_1, β_2, β_3, β_4, β_5, and β_6) and model R^2 for each location (Table 1). We mapped coefficients with *p*-values < 0.05 and R^2 values of the local and global kernel bandwidth GWR models using contour plots in ArcView 3.2 (Environmental Systems Research Institute Inc.; Fig. 6) to illustrate the spatial heterogeneity of these predictor variables.

Contour plots of localized parameter estimates from the local kernel bandwidth GWR model permit visualization of their influence on deer density across the study area. Under the impact of snow depth (Fig. 6a),
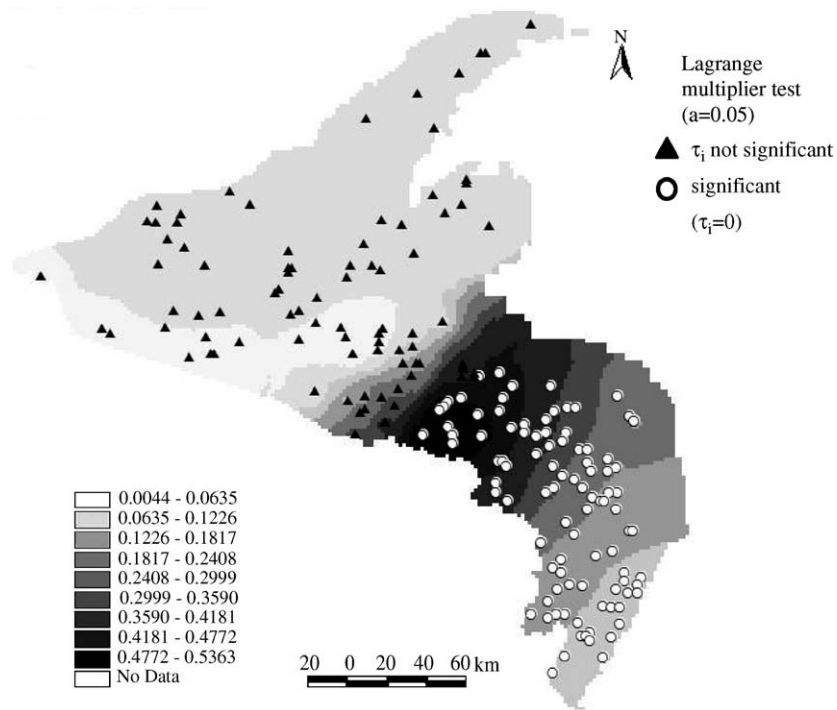
Fig. 5. Contour plot of local kernel bandwidth values with the Lagrange Multiplier (LM) test in the GWR model.

deer density was high in the center and southern parts of the UP (Fig. 2). Although the influence of Lake Superior caused snow depth to be deeper in the northern UP than in the southern UP, there were several factors predicted to limit the influence of snow depth on deer distribution using the local kernel bandwidth model. For example, patch size coefficients of variances of northern hardwoods and wetland hardwood/conifers were higher in the northern UP compared with the southern UP indicating greater importance of patches edges (foraging areas) in the north (Fig. 6c and e). The larger mixed pine patches in the northern UP also had greater influence on deer density than mixed pine patch size did in the southern UP (Fig. 6g). This is primarily because there are fewer cedar swamps, the preferred cover type for deeryards, in the northern UP. White cedar patch size had a greater influence on the distribution of deer in the southern part of UP than in the north, as indicated by higher values of its localized coefficient in the south (Fig. 6i).

Table 1
Estimated model coefficients with local and global kernel bandwidth

	τ	$\beta_0(u_i, v_i)$ (Intercept)	$\beta_1(u_i, v_i)$ (HV)	$\beta_2(u_i, v_i)$ (WV)	$\beta_3(u_i, v_i)$ (MA)	$\beta_4(u_i, v_i)$ (CA)	$\beta_5(u_i, v_i)$ (log(PA))	$\beta_6(u_i, v_i)$ (SD)	R^2
Global kernel bandwidth GWR model									
Max	2.2446	0.9411	0.0016	0.0091	0.0071	0.0831	0.3242	0.1108	0.85
Min	2.2446	−4.8575	0.0004	0.0018	0.0020	0.0174	−0.1322	−0.0387	0.48
Local kernel bandwidth GWR model									
Max	0.5366	0.2208	0.0012	0.0039	0.0033	0.0439	0.1680	−0.0172	0.41
Min	0.0032	0.1287	0.0010	0.0034	0.0027	0.0413	0.1306	−0.0208	0.28

Note: HV, northern hardwood patch size coefficient of variance; WV, wetland hardwood/conifer patch size coefficient of variance; MA, patch area of mixed pine; CA, patch area of white cedar canopy cover>70%; PA, average perimeter-area ratio; SD, snow depth.

As mentioned above, the local parameter estimates could be more statistically and ecologically interpretable than those from the global bandwidth model. This is also the case for the plotted estimates (Fig. 6a–j).

The GWR model with global kernel bandwidth is less capable of incorporating different effects of snow depth and factors that can buffer winter severity, such as the availability of foraging areas.
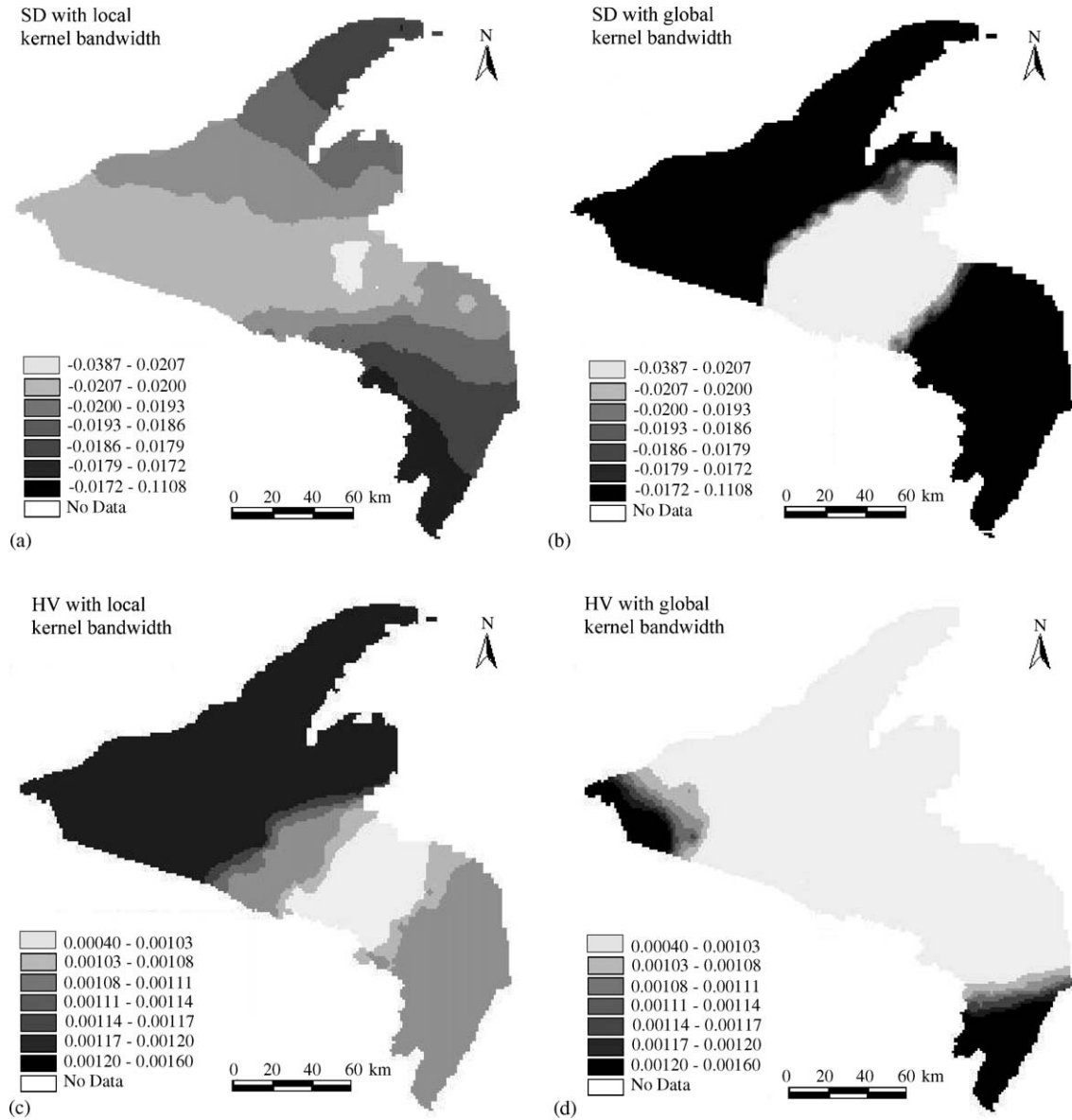

Fig. 6. Localized parameter estimates for ecological variables included in the GWR model including (a) snow depth (SD) by local kernel bandwidth, (b) snow depth (SD) by global kernel bandwidth, (c) northern hardwood patch size coefficient of variance (HV) by local kernel bandwidth, (d) northern hardwood patch size coefficient of variance (HV) by global kernel bandwidth, (e) wetland hardwood/conifer patch size coefficient of variance (WV) by local kernel bandwidth, (f) wetland hardwood/conifer patch size coefficient of variance (WV) by global kernel bandwidth, (g) patch area of mixed pine (MA) by local kernel bandwidth, (h) patch area of mixed pine (MA) by global kernel bandwidth, (i) patch area of white cedar canopy cover >70% (CA) by local kernel bandwidth, (j) patch area of white cedar canopy cover >70% (CA) by global kernel bandwidth, (k) the localized R^2 by local kernel bandwidth, (l) the localized R^2 by global kernel bandwidth.
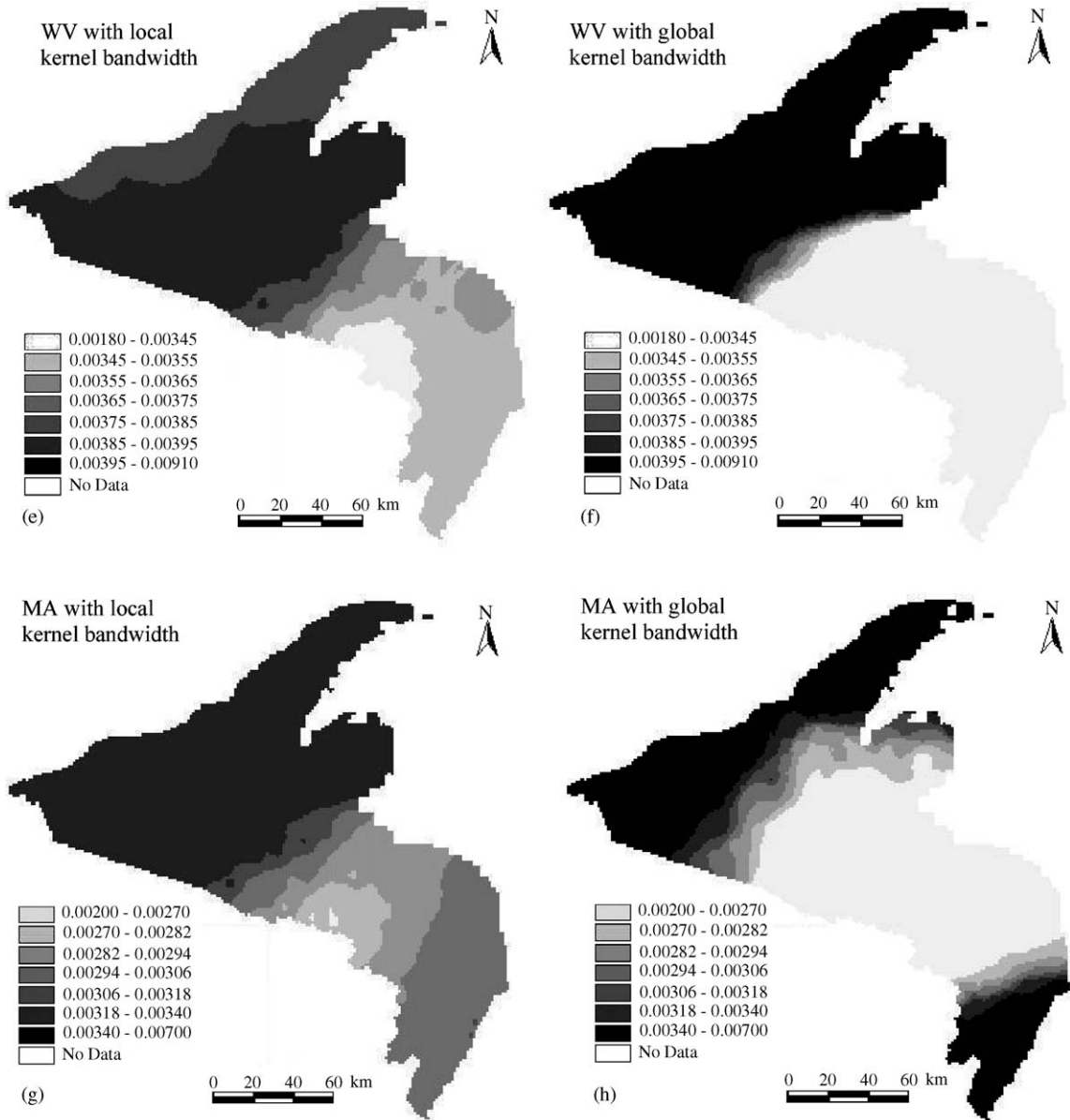
Fig. 6. (*Continued*)

However, the localized R^2 obtained from the global kernel bandwidth GWR model was greater than that from the local kernel bandwidth GWR model (Fig. 6k and l). This might be a result of ignoring the finer scale local spatial variation by the global kernel bandwidth. Regardless of their differences, the spatial patterns were similar. Both models fit better in the northern parts

of UP (higher localized R^2 values) than in the southern parts of UP.

3.4. Local nonstationarity test

The parameter estimates of the global kernel bandwidth GWR model were not constant (i.e., nonstation-
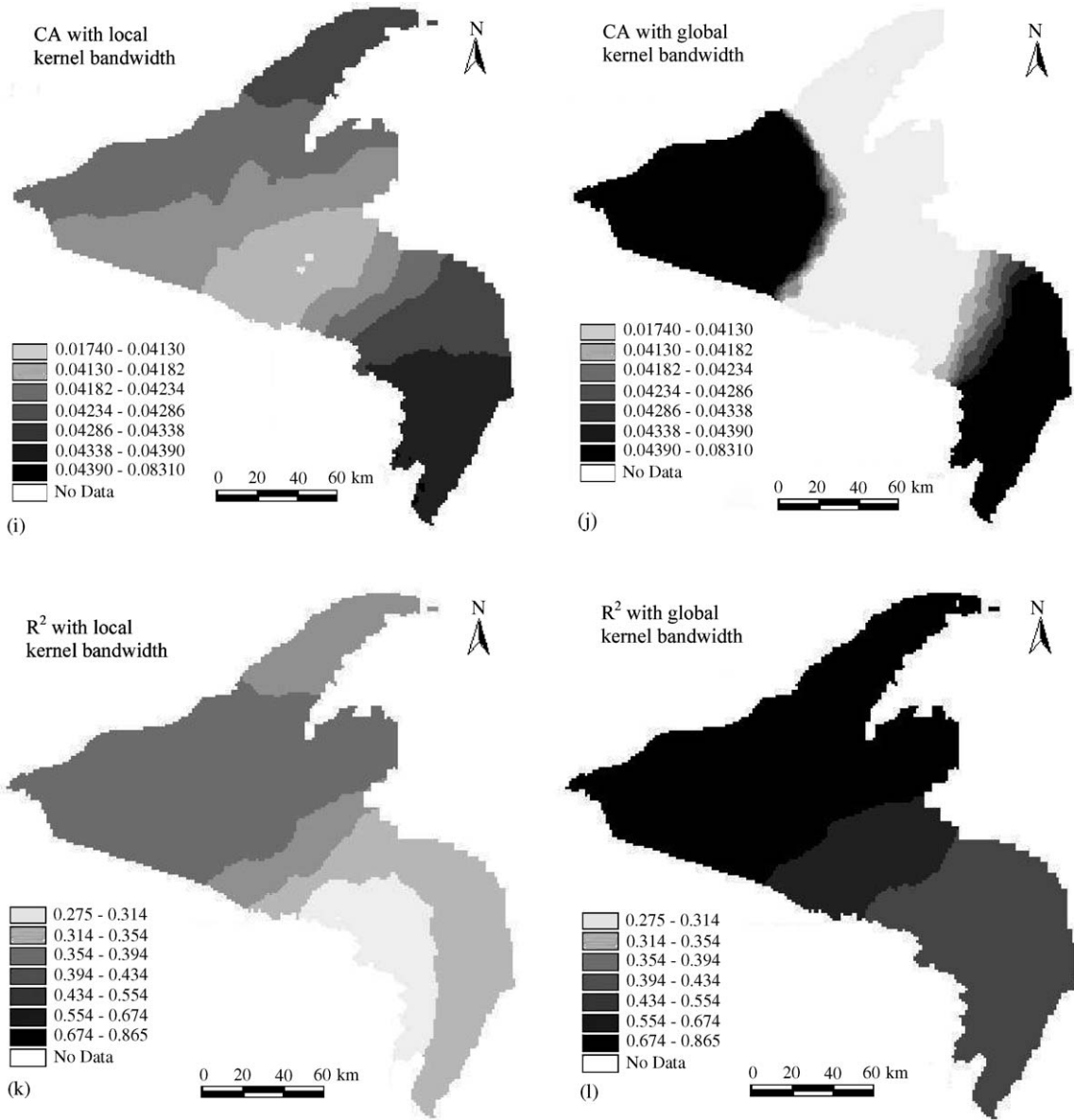
CA with local
kernel bandwidth

N

0.01740 - 0.04130
0.04130 - 0.04182
0.04182 - 0.04234
0.04234 - 0.04286
0.04286 - 0.04338
0.04338 - 0.04390
0.04390 - 0.08310
No Data

0   20   40   60 km

(i)

CA with global
kernel bandwidth

N

0.01740 - 0.04130
0.04130 - 0.04182
0.04182 - 0.04234
0.04234 - 0.04286
0.04286 - 0.04338
0.04338 - 0.04390
0.04390 - 0.08310
No Data

0   20   40   60 km

(j)

R^2 with local
kernel bandwidth

N

0.275 - 0.314
0.314 - 0.354
0.354 - 0.394
0.394 - 0.434
0.434 - 0.554
0.554 - 0.674
0.674 - 0.865
No Data

0   20   40   60 km

(k)

R^2 with global
kernel bandwidth

N

0.275 - 0.314
0.314 - 0.354
0.354 - 0.394
0.394 - 0.434
0.434 - 0.554
0.554 - 0.674
0.674 - 0.865
No Data

0   20   40   60 km

(l)

Fig. 6. (*Continued*).

ary) across the study area according to the local parameter variation test (p-values <0.05, Table 2). Rejection of the null hypothesis confirms that the local parameter estimates varied from case to case across the study area (nonstationarity of parameter estimates). In the case of the local kernel bandwidth GWR model, t-tests for locational heterogeneity of the local kernel band-

width GWR model coefficients indicated that not all parameter estimates were significant ($P > 0.05$). The t-tests for four parameter estimates, including northern hardwood patch size coefficient of variance, wetland hardwood/conifer patch size coefficient of variance, patch area of mixed pine and patch area of white cedar, demonstrated that locational heterogeneity did exist

Table 2
F-tests for the local nonstationarity of parameter estimates within GWR using the global kernel bandwidth

Parameter	*P*-value
Intercept	<0.0001
HV	0.0004
WV	<0.0001
MA	<0.0001
CA	0.0004
log(PA)	0.0002
SD	<0.0001

Note: The definitions of HV, WV, MA, CA, PA, and SD are the same as those in Table 1.

for these predictor variables ($p < 0.01$). In the case of average perimeter-area ratio, 69 out of 181 locations were not significant ($\alpha = 0.05$). For the local parameter estimates of snow depth, 82 out of 181 locations were not significant. All local estimates of intercepts were not significant. Regardless of using the local kernel bandwidth or the global kernel bandwidth in the GWR models, the parameter estimates were not constant over space according to the local nonstationarity test.

3.5. Improvement of GWR over OLS

The global kernel bandwidth GWR model performed better than the OLS model, according to an approximate *F*-test (Table 3). The model parameter estimates of Eq. (2) were thus better modeled as a spatially variable parameter from subarea to subarea within the whole region. In other words, the simple linear relationship between deer density and ecological variables was not constant across the study area.

The LM test indicated that 94 local kernel bandwidths were significantly different from 0 (Fig. 5). Hence, at these 94 locations the local kernel bandwidth GWR model performed better than the OLS model.

Table 3
Goodness-of-fit test for improvement in model fit of GWR over OLS

	Source	SS	DF	MS	*F*	*P*-value
OLS	Residuals	75.8	7			
GWR	Improvement	15.6	11.62	1.3419		
GWR	Residuals	60.2	162.38	0.3706	3.621	0.0282

SS: sum of squares; DF: effective degree of freedom; MS: mean square; *F*: *F*-statistic; *P*-value: the probability of *F*-distribution with degrees of freedom 7 and 11.62.

The remaining 87 locations were not significant. These results were consistent with results of the location heterogeneity test. Plots of these data (Fig. 5) indicated: (1) there was a clear boundary between the significant and nonsignificant sampling units; (2) there was a lack of spatial nonstationarity in the northern UP, although spatial nonstationarity existed in the southern UP; and (3) relative winter deer density was higher in the nonstationary southern part of the study region.

4. Discussion

By comparing an OLS model and two GWR models, we found that spatial heterogeneity in the relationships of deer distribution to patch metrics and other variables (e.g., climate) could be more effectively explored using GWR. The GWR models not only produced better predictions of deer density than the traditional OLS model but also provided useful information on the nature of the deer distribution variation caused by neighboring environmental factors. Although differences existed between the results of the local and global GWR models, the spatial patterns of the parameter estimates showed the same general trends in parameter variation across the study area. Visualization of the two GWR model coefficients and statistics in a GIS highlighted the spatial distribution of the multivariate relationship under study.

4.1. Ecological variables

Although we used pellet counts for obtaining the deer density, the adequacy of using pellet counts to estimate deer density has been questioned (Smart et al., 2004). The actual relationship between deer density and pellet group density is much more complex and is impacted by factors, such as, weather, diet, and composition of the deer herd. However, experiments have shown that the simple relationship used in our study (Eq. (1)) is a reasonable approximation of the true relationship between pellet group density and actual deer density (Eberhardt and VanEtten, 1956). More complex estimates could reduce the interpretability of results if not precisely parameterized.

The predictor variables were ecologically interpretable. Snow depth is known to affect the distribution of deer in wintertime (Kirchhoff and Schoen, 1987;

Fleming et al., 1994). White cedar canopy cover >70% and mixed conifer stands serve as deeryards in the UP (Blouch, 1984, p. 339). Large northern hardwood and wetland hardwood/conifer patch size coefficients of variance (HV and WV) indicate that many forest edges, the preferred foraging areas of deer, are available (Chang et al., 1995; Sheehy and Vavra, 1996). Patch size, patch size coefficient of variance, average perimeter-area ratio and snow depth have been widely used as predictor variables in various deer distribution models (e.g., Severinghaus, 1972; Fleming et al., 1994; Lovallo and Tzilkowski, 2003; White et al., 2004).

As snow depth increases, it is not only hard for deer to find food but also difficult for them to walk. Thus, snow-depth should have a negative effect on deer density as consistently predicted in the local kernel bandwidth GWR model. However, the global kernel bandwidth GWR model occasionally predicted a positive sign for the snow depth parameter that is difficult to interpret ecologically. Using the global kernel bandwidth, there were wide variations and inconsistencies in the signs of parameter estimates. Three out of seven parameter estimates for the global kernel bandwidth GWR model ranged from negative to positive values, making interpretation difficult.

4.2. Kernel bandwidth

In contrast to the global kernel bandwidth model, the parameter estimates of the local kernel bandwidth GWR model varied little and the local kernel bandwidths differed from location to location. For example, the range of parameter estimates of the white cedar patch size obtained from the global kernel bandwidth GWR model was about 24 times larger than that obtained from the local kernel bandwidth GWR model (Table 1). Other parameter estimates for both models showed similar ranges of variation. The low variation of local kernel bandwidth model was similar to the OLS model estimates (Eq. (6)), indicating local variation close to these estimates. Visual assessment of the contour maps of the significant parameter estimates indicated the existence of spatial heterogeneity, however, it was not to the extent emphasized by the global kernel bandwidth GWR model. A contour plot of the local kernel bandwidth revealed that the local kernel bandwidth varied continuously over space rather than

being constant (Fig. 5). Therefore, the constant global kernel bandwidth obtained from cross-validation might not be locally reliable.

In general, if the bandwidth is large, the weights decay quickly with distance and the values of the regression coefficients change rapidly over space (Fig. 7). Smaller bandwidths thus produce smoother results (Brunsdon et al., 1996). In other words, the parameter estimates would be similar if they are close to each other over space. Our results indicated that the GWR model with global kernel bandwidth generally had a small number of neighbors because of the large bandwidth. The effect was to cause great overestimation of spatial heterogeneity and a consequent underestimation of neighboring values due to steeper rates of decay in the kernel function (Fig. 7). In comparison, the GWR model with local kernel bandwidth overcame these shortcomings by changing with the local spatial trend (e.g., the variation of white cedar patch size). The large local kernel bandwidth in the center of the study region (dark area) indicated that the local spatial variation of the landscape features was higher there than that in other areas (light area, Fig. 5). This variation was averaged in the global GWR model.

4.3. Local nonstationarity

The rejection of the null hypothesis for local nonstationarity in the global kernel bandwidth GWR model might be due to the global (constant) kernel bandwidth and/or the availability of a small number of neighbors within this bandwidth used to estimate parameter values. In contrast, the OLS model completely ignored local nonstationarity by not including spatial information in the model weighting function. Parameter estimates obtained with the local kernel bandwidth were between the values of the global kernel bandwidth GWR model, which unadequately accounted for spatial heterogeneity due to the global kernel bandwidth and the OLS model, which ignored spatial heterogeneity. Therefore, the local kernel bandwidth GWR model fit the data better than the global kernel bandwidth GWR model and the OLS model.

Theoretically, local nonstatitionarity is caused by an imperfect data set with missing information (Fotheringham, 1997). If all important variables were collected and the data set were complete, nonstationarity would disappear. However, perfect data sets are

Note: d_{ij} is the distance between observation i and its neighboring observation j
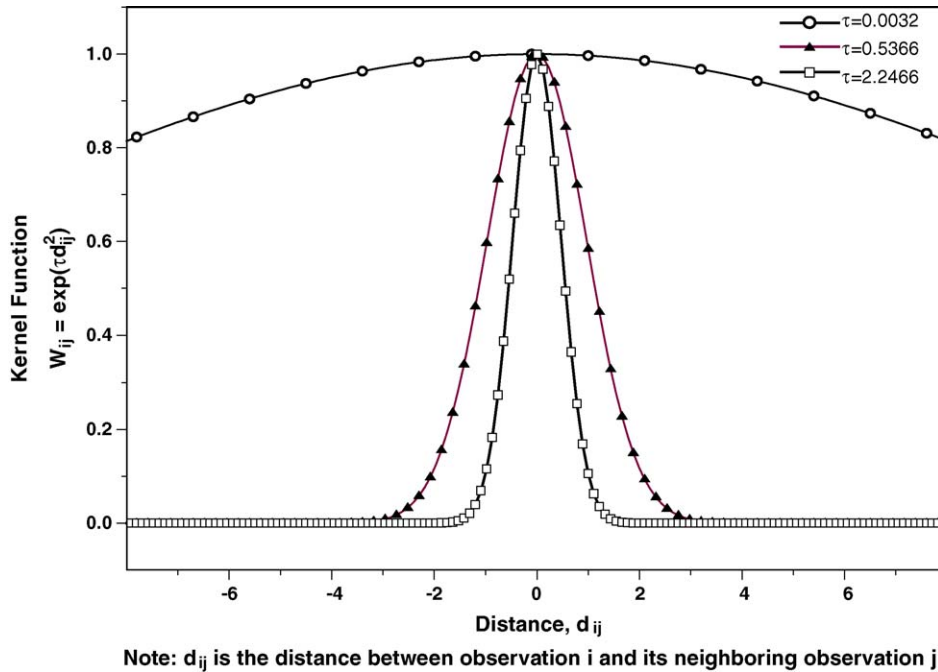
Fig. 7. Comparison of different rates of decay in spatial heterogeneity with different kernel bandwidths.

generally unavailable. For example, modeled deer distribution is affected by sampling design, ecological preferences of deer, the location, frequency, duration and intensity of human disturbance, and environmental stochasticity, among other factors. Additionally, there is often a positive spatial autocorrelation among neighboring deer populations as a consequence of association with microsite (e.g., topography, snow gradient) heterogeneity that decreases with distance. Because researchers often do not have complete information on topographical characteristics and management history for the study area, it is helpful to apply GWR to reveal spatial nonstationarity, highlight the gaps in data, and direct future data collection. Incorporating spatial information into local modeling methods can thus greatly improve model predictability.

4.4. Potential of GWR for modeling deer population dynamic

A number of deer population models have been developed without considering spatial heterogeneity and spatial interaction among environmental variables (Xie et al., 1999; Radeloff et al., 1999; Jensen and Miller, 2001; Peterson et al., 2003; Yamada et al., 2003; Grund and Woolf, 2004). These deer population models require reproduction, sex ratio, age structure, harvest, and mortality data (Xie et al., 1999, 2001; Peterson et al., 2003; Grund and Woolf, 2004). However, these data are difficult to collect and often site specific. Because local modeling techniques such as GWR take spatial heterogeneity into account and generate a better model fit (e.g., the improvement of GWR over OLS) and more accurate prediction (Fotheringham and Brunsdon, 1999), we suggest future population dynamic models should take GWR into consideration.

5. Conclusions

The comparison between the local and global kernel bandwidth GWR models indicates that the local kernel bandwidth GWR model is preferable to the global kernel bandwidth GWR model. The basic assumptions of the local and global kernel bandwidth GWR models were different, therefore, a statistical test cannot
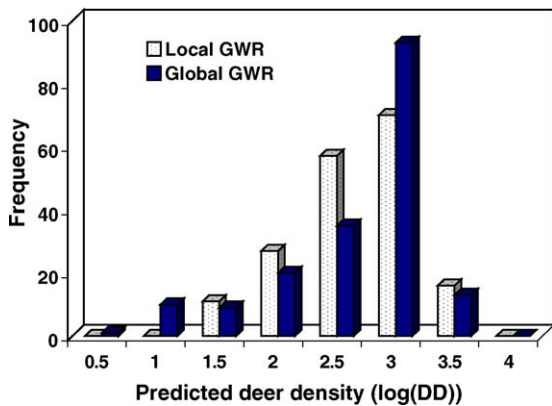
Fig. 8. The comparison of predicted deer densities obtained from the local and global kernel bandwidth GWR models (DD: deer density).

currently be conducted (Pàez et al., 2002a,b). However, direct comparisons between those two models showed large differences in predictions (Fig. 8). Spatial heterogeneity was not as precisely modeled by the global kernel bandwidth GWR model due to the constant kernel bandwidth that ignored local spatial variation (Fotheringham et al., 1998). The global kernel bandwidth GWR model primarily addresses spatial parametric nonstationarity, while the local kernel bandwidth GWR model was used to account for spatial heterogeneity in a spatial context (Pàez et al., 2002a,b). In addition, the localized parameter estimates obtained from the local kernel bandwidth GWR model were easier to interpret statistically and ecologically.

The results of these analyses show that GWR models can serve as useful tools for exploratory and predictive spatial data analysis. Some statistics, such as kernel bandwidth and local nonstationarity test, can also serve as useful measurements for deer management and natural resources conservation. This methodology also allows the influence of microsite variation and management activities on deer to be evaluated, tested, and readily displayed with GIS or statistical graphic packages to provide land managers or decision makers with useful information for management purposes. For example, management activities can be targeted to indirectly affect deer density by changing land cover characteristics (e.g., vegetation composition and structure) or to directly control deer density (e.g., hunting) in a particular area.

References

Andersen, M., 1992. Spatial analysis of two-species interactions. Oecologia 91, 134–140.

Anselin, L., 1988. Spatial Econometrics: Methods and Models. Kluwer Academic Publishers, Dordrecht, 284 p.

Anselin, L., Griffith, D.A., 1988. Do spatial effects really matter in regression analysis. Papers of the Regional Science Association 65, 11–34.

Anselin, L., 1990. What is special about spatial data? Alternative perspectives on spatial data analysis. In: Griffith, D. (Ed.), Spatial Statistics: Past, Present, and Future. Institute of Mathematical Geography, Ann Arbor, Michigan, pp. 63–77.

Augustin, N.H., Mugglestone, M.A., Buckland, S.T., 1996. An autologistic model for the spatial distribution of wildlife. J. Appl. Ecol. 33, 339–347.

Blouch, R.I., 1984. Northern Great Lakes states and Ontario forests. In: Halls, L.K. (Ed.), White-Tailed Deer Ecology and Management. Stackpole Books, Harrisburg, PA, USA, pp. 391–410.

Bowyer, R.T., Stewart, K.M., Wolfe, S.A., Blundell, G.M., Lehmkuhl, K.L., Joy, P.J., McDonough, T.J., Kie, J.G., 2002. Assessing sexual segregation in deer. J. Wildl. Manage. 66, 536–544.

Breusch, T.S., Pagan, A.R., 1979. A simple test for heteroscedasticity and random coefficient variation. Econometrica 47, 1287–1294.

Breusch, T.S., Pagan, A.R., 1980. The Lagrange multiplier test and its applications to model specification in econometrics. Rev. Econ. Stud. 48, 239–253.

Brunsdon, C.A., Fotheringham, A.S., Charlton, M.E., 1996. Geographically weighted regression: a method for exploring spatial nonstationarity. Geographical Anal. 28, 281–298.

Brunsdon, C.A., Fotheringham, A.S., Charlton, M.E., 1998. Geographically weighted regression—modeling spatial nonstationary. Statistician 47, 431–443.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, 446 pp.

Chang, K., Verbyla, D.L., Yeo, J.J., 1995. Spatial analysis of habitat selection by Sitka Black-Tailed Deer in southeast Alaska, USA. Environ. Manage. 19, 579–589.

Coppolillo, P.B., 2000. The landscape ecology of pastoral herding: spatial anylsys of land use and livestock production in East Africa. Hum. Ecol. 28, 527–560.

Doepker, R., Beyer, D.E., Donovan, M., 1994. Deer population trends in Michigan's Upper Penninsula: Michigan Department of Natural Resources; Wildlife Division Report 3254.

Eberhardt, L.L., VanEtten, R.C., 1956. Evaluation of the pellet-group count as a deer census method. J. Wildl. Manage. 20, 70–74.

Fleming, D.M., Schortemeyer, J., Ault, J., 1994. Distribution, abundance and demography of white-tailed deer in the Everglades. In: Dennis Jordan (Ed.), Proceedings of the Florida Panther Conference, Ft. Myers Fla., November 1994. U.S. Fish and Wildlife Service, pp. 494–503.

Fotheringham, A.S., 1997. Trends in quantitative methods. I. Stressing the local. Prog. Hum. Geography 21, 88–96.

Fotheringham, A.S., Brunsdon, C., Charlton, M.E., 1998. Geographically weighted regression: a natural evolution of the expansion method for spatial data analysis. Environ. Planning A 30, 1905–1927.

Fotheringham, A.S., Brunsdon, C., 1999. Local forms of spatial analysis. Geographical Anal. 31, 340–358.

Fotheringham, A.S., Brunsdon, C., Charlton, M.E., 2000. Quantitative Geography: Perspectives on Spatial Data Analysis. SAGE Publications, 270 pp.

Fotheringham, A.S., Brunsdon, C., Charlton, M.E., 2002. Geographically Weighted Regression: The Analysis of Spatially Varying Relationships. John Wiley & Sons, New York, 269 pp.

Getis, A., Franklin, J., 1987. Second-order neighborhood analysis of mapped point patterns. Ecology 68, 473–477.

Gribko, L.S., Hohn, M.E., Ford, W.M., 1999. White-tailed deer impact on forest regeneration: modeling landscape-level deer activity patterns. In: Proceedings of the 12th Central Hardwood Forest Conference, 28 February, 1-2 Mar.

Grund, M.D., Woolf, A., 2004. Development and evaluation of an accounting model for estimating deer population sizes. Ecol. Model 180, 345–357.

Hair, J.F., Anderson, R.E., Tatham, R.L., Black, W.C., 1995. Multivariate Data Analysis. Englewood cliffs, New Jersey, 745 pp.

Hill, H.R., 1999. The 1999 deer pellet group surveys. Michigan Department of Natural Resources. Wildlife bureau report No. 3292.

Hosmer, D., Lemeshow, S., 1989. Applied Logistic Regression. Wiley-Interscience, New York, 322 pp.

Jensen, A.L., Miller, D.H., 2001. Age structured matrix predation model for the dynamics of wolf and deer populations. Ecol. Model 141, 299–305.

Kie, J.G., Bowyer, R.T., Nicholson, M.C., Boroski, B.B., Loft, E.R., 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. Ecology 83, 530–544.

Kimerling, A.J., 2002. Predicting data loss and duplication when resampling from Equal-Angle grids. Cartography Geographic Inf. Sci. 29, 111–126.

Kirchhoff, M.D., Schoen, J.W., 1987. Forest cover and snow: implications for deer habitat in southeast Alaska. J. Wildl. Manage. 51, 28–33.

Leung, Y., Mei, C., Zhang, W., 2000. Satistical tests for nonstationarity based on the geographically weighted regression model. Environ. Planning A 32, 9–32.

Li, H., Reynolds, J.F., 1994. A simulation experiment to quantify spatial heterogeneity in categorical maps. Ecology 75, 2446–2455.

Liu, J., Taylor, W.W., 2002. Integrating Landscape Ecology and Resource Management. Cambridge University Press, Cambridge, UK.

Lovallo, M.J., Tzilkowski, W.M., 2003. Abundance of white-tailed deer within valley forge national historical park and movements related to surrounding private lands. School of forest resources, The Pennsylvania State University, Technical report NPS/NERCHAL/NRTR-03/091.

Mazerolle, M.J., Villard, M., 1999. Patch characteristics and landscape context as predictors of species presence and abundance: a review. Ecoscience 6, 117–124.

McShea, W.J., Underwood, H.B., Rappole, J.H., 1997. The Science Of Overabundance: Deer Ecology And Population Management. Smithsonian Institution Press.

Nelson, M.E., Mech, L.D., 1981. Deer social organization and wolf predation in northeastern Minnesota. Wildl. Monogr. No. 77, 53 pp.

Ozoga, J.J., Gysel, L., 1972. Response of white-tailed deer to winter weather. J. Wildl. Manage. 36, 893–896.

Pàez, A., Uchida, T., Miyamoto, K., 2002a. A general framework for estimation and inference of geographically weighted regression models. 1. Location-specific kernel bandwidths and a test for locational heterogeneity. Environ. Planning A 34, 733–754.

Pàez, A., Uchida, T., Miyamoto, K., 2002b. A general framework for estimation and inference of geographically weighted regression models. 2. Spatial association and model specification tests. Environ. Planning A 34, 883–904.

Pearce, C.M., 1987. GIS-based habitat modeling using logistic multiple regression: a study of the Mt. Graham red squirrel. Photogr. Eng. Rem. Sens. 57, 1475–1486.

Peterson, M.N., Grant, W.E., Lopez, R.R., Silvy, N.J., 2003. Implications of fetal sex ratio hypotheses in endangered populations: simulated dynamics of Florida Key deer, Florida, USA. Ecol. Model 165, 209–220.

Radeloff, V.C., Pidgeon, A.M., Hostert, P., 1999. Habitat and population modeling of roe deer using an interactive geographic information system. Ecol. Model. 114, 287–304.

Rempel, R.S., Carr., A.P., 2003. Patch Analyst extension for ArcView: version 3. http://flash.lakeheadu.ca/~rrempel/patch/index.html.

Ripley, B.D., 1979. Tests of 'randomness' for spatial point pattern. J. R. Stat. Soc. B 41, 368–374.

Ripley, B.D., 1981. Spatial Statistics. John Wiley & Sons, New York, 252 p.

Severinghaus, C.W., 1972. Weather and the deer. Conservationist 27, 28–31.

Sheehy, D.P., Vavra, M., 1996. Ungulate foraging areas on seasonal rangeland in northeastern Oregon. J. Range Manage. 49, 16–23.

Shi, H., Zhang, L., 2003. Local analysis of tree competition and growth. For. Sci. 49, 938–955.

Smart, J.C.R., Ward, A.I., White, P.C.L., 2004. Monitoring woodland deer populations in the UK: an imprecise science. Mamal Rev. 34, 99–114.

Stankovski, V., Debeljak, M., Bratko, I., Adamic, M., 1998. Modelling the population dynamics of red deer (*Cervus elaphus* L.) with regard to forest development. Ecol. Model. 108, 145–153.

Sterner, R.W., Ribic, C.A., Schatz, G.E., 1986. Testing for life historical changes in spatial patterns of four tropical tree species. J. Ecol. 74, 621–633.

VanDeelen, T.R.V., Campa, H., Hamady, M., Haufler, J.B., 1998. Migration and seasonal range dynamics of deer using adjacent deeryards in Northern Michigan. J. Wildl. Manage. 62, 205–213.

Verme, L.J., 1973. Movements of white-tailed deer in Upper Michigan. J. Wildl. Manage. 37, 545–552.

White, P.C.L., Smart, J.C.R., Böhm, M., Langbein, J., Ward, A.I., 2004. Economic impacts of wild deer in the east of England. Central Science Laboratory, Woodchester Park, Tinkley Lane, Nympsfield, Stonehouse, Gloucestershire, GL10 3UJ, UK.

Wiens, J.A., 2001. The landscape context of dispersal. In: Clobert, J., Danchin, E., Dhondt, H.H., Nichols, J.D. (Eds.), Dispersal. Oxford University Press, Oxford, pp. 96–109.

Xie, J., Hill, H.R., Winsterstein, S.R., Campa III, H., Doepker, R.V., Deelen, T.R., Liu, J., 1999. White-tailed deer management options model (DeerMOM) design, quantification and application. Ecol. Model. 124, 121–130.

Xie, J., Liu, J., Doepker, R., 2001. DeerKBS: a knowledge-based system for white-tailed deer management. Ecol. Model. 140, 177–192.

Yamada, K., Elith, J., McCarthy, M., Zerger, A., 2003. Eliciting and integrating expert knowledge for wildlife habitat modelling. Ecol. Model. 165, 251–264.

Zhang, L., Shi, H., 2004. Local modeling of tree growth by geographically weighted regression. For. Sci. 50, 225–244.