

Modeling White-tailed Deer Activity Patterns Across Forested Landscapes

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Abstract.—White-tailed deer (*Odocoileus virginianus*) herbivory has been identified as a major impediment to the survival and growth of forest regeneration in the northeastern United States. As a supplement to direct control of deer densities through hunting, it may be possible for land managers to manipulate habitat and browsing pressure through carefully planned timber harvest. We are developing methods to relate deer habitat use patterns to regeneration condition and complexity across large landscapes. The preliminary research presented here involved development of methodology to efficiently and effectively model deer habitat use patterns across forested landscapes using fecal pellet groups as an activity index.

Work was conducted in summer 1997 on the 3,078-ha West Virginia University Forest (WVUF) in north-central West Virginia and the 3,413-ha Westvaco Wildlife and Ecosystem Research Forest (WERF) in the south-central portion of the state. Fecal pellet group counts were conducted on geolocated 1.72-m radius circular plots at an intensity of approximately 1 plot per 2.4 ha. We used variography to investigate spatial dependence in the data. Deposition patterns were modeled using geographic information systems (GIS) technology and a spatial statistics technique known as two-dimensional ordinary point kriging. Variography revealed spatial contagion in the WVUF data that could be accurately modeled using this methodology. The resulting interpolated probability map is of high potential value in the long-term monitoring of deer activity patterns across this forested landscape. Results on the WERF indicated that sampling intensity was too coarse to allow modeling of strong localized dependence in the data.

Excessive white-tailed deer (*Odocoileus virginianus*) herbivory, or browsing, has been identified as a major impediment to the survival and growth of tree seedlings and herbaceous plants in the northeastern United States (Shafer *et al.* 1961, Tierson *et al.* 1966, Jordan 1967, Alverson *et al.* 1988, Tilghman 1989, Trumbull *et al.* 1989). Browsing can affect forest regeneration by reducing seedling numbers, reducing seedling height, altering species composition, delaying stand establishment, or causing complete regeneration failure (Redding 1987). Of particular concern to forest managers are conversions of woody understories to ferns and grasses (Marquis 1974, Horsely and Marquis 1983) and the elimination of highly valued commercial tree species such as northern red oak (*Quercus rubra*) from the pool of large advance regeneration under mature forest canopies (Marquis *et al.* 1976). Severely impacted forest ecosystems are devoid of most understory plants that are palatable to deer and may exhibit an overall reduction in animal diversity (deCalesta 1994).

Deer herbivory research conducted to date suggests that deer population densities in many forested landscapes should be reduced (Behrend *et al.* 1970, Marquis 1981, Storm *et al.* 1989, Bowersox *et al.* 1993, McCormick *et al.* 1993). However, the public demand for deer hunting opportunity often outweighs concerns about browsing impacts; state wildlife agencies are consequently reluctant to lower deer densities to suggested levels (Sheffer 1987).

Rather than attempting to control deer densities directly through harvest, it may be possible to manage forested landscapes to reduce browsing pressure and regeneration damage. The manipulation of the spatial distribution of clearcuts has been suggested as one means of accomplishing this objective (Ford *et al.* 1994). Deer extensively forage in recent clearcuts during spring and summer when succulent leaves and new growth are available (Wentworth *et al.* 1990, Ford *et al.* 1993). In the central and southern Appalachians, the availability of clearcuts has been found to increase carrying capacity of the surrounding forest and reduce browsing pressure on forested understories during the summer (Johnson *et al.* 1995). Careful planning of the intensity, timing, and location of timber harvest areas may allow managers to draw deer away from forested understories while maintaining the population at a sufficient density to provide adequate hunting opportunity.

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Currently, a lack of deer herbivory research conducted at the landscape level constrains the development of forest management recommendations. Most studies have considered localized, or stand-level, effects of deer browsing. Investigators have considered the impacts of deer in contiguous closed-canopy forests (Marquis 1981), in small isolated woodlots (Storm *et al.* 1989, Bowersox *et al.* 1993), in recently clearcut areas (Marquis and Grisez 1978), or after specific stand treatments such as thinnings (McCormick *et al.* 1993). Typically, such research has involved comparisons of areas with varying densities of deer or the use of fencing and barriers to manipulate deer impacts. Work at larger spatial scales (500- to 1,000-ac blocks) was recently initiated in Pennsylvania (Stout *et al.* 1995). However, the highly fragmented, severely browsed forests of Pennsylvania may not be comparable to the more continuous, less intensively browsed forests found elsewhere in the Appalachian region.

In 1997, we initiated a study designed to relate deer habitat use patterns to woody regeneration condition and complexity across landscapes dominated by relatively continuous closed-canopy second-growth hardwood forest. This paper reports the results of the first phase of study in which we developed a method of quantifying landscape-level deer habitat use patterns using fecal pellet group counts as an activity index. Generally, pellet groups are counted on either rectangular belt transects (Bennett *et al.* 1940, Robinette *et al.* 1958, Fuller 1991) or circular plots of various dimensions (Eberhardt and Van Etten 1956, Robinette *et al.* 1958, Van Etten and Bennett 1965). Counts of fecal pellet groups are widely used to census deer populations and to determine habitat use (Neff 1968). Average counts within management units or habitat types are compared as relative indices of deer abundance or are used with defecation rate to estimate population densities. Bennett *et al.* (1940) found that deer defecate close to feeding areas, indicating that high densities of fecal pellets may be associated with high levels of herbivory.

Traditionally, spatial patterns of pellet group deposition are not considered. However, if the spatial dependency among fecal pellet counts made at a large number of discreet points throughout a forested landscape is strong enough to be modeled, the relationship could be used to estimate pellet count densities at unsampled locations. A map, or data layer, of predetermined spatial resolution would result. The field of geology offers techniques, termed geostatistics, that can be used to quantify the inherent spatial dependencies in data and use them to create interpolated data coverages. Although developed to model petroleum and mineral reserves, geostatistics have also been used in the modeling of ecological data (Robertson 1987, Rossi *et al.* 1992, Pelletier and Parma 1994, Villard and Maurer 1996). One of these techniques, *kriging*, has been applied outside of the geological

sciences to model insect outbreaks (Kemp *et al.* 1989, Liebhold *et al.* 1991, Hohn *et al.* 1993, Gribko *et al.* 1995), forest biomass and nutrient cycles (Pauley *et al.* 1996), and old-growth forest characteristics (Biondi *et al.* 1994).

The purpose of this study was to determine if fecal pellet group counts made at discrete points could be used to model deer activity patterns across a forested landscape. Specific objectives included: (1) to quantify the spatial dependence inherent in deer fecal group deposition, and (2) to determine the suitability of geostatistical techniques, specifically two-dimensional ordinary point kriging, in mapping white-tailed deer use of forested landscapes.

METHODS

Study Areas

The study was conducted on two sites: the 3,078-ha West Virginia University Forest (WVUF) in Monongalia and Preston Counties, WV, and the 3,413-ha Westvaco Wildlife and Ecosystem Research Forest (WERF) in Randolph County, WV. The WVUF is located on the westernmost anticline of the Allegheny Mountains. Elevations range from 318 to 796 m. The tract is covered by closed-canopy 70- to 80-year-old hardwood forest; no more than 200 ha have been impacted by timber harvest or major canopy disturbance in the past 20 years. Four forest types as classified by SAF (Eyre 1980) have been identified on the WVUF: yellow-poplar (*Liriodendron tulipifera*)-white oak (*Quercus alba*)-northern red oak (*Quercus rubra*); white oak-black oak (*Quercus velutina*)-northern red oak; chestnut oak (*Quercus prinus*); and yellow-poplar (*Liriodendron tulipifera*). The two types containing yellow-poplar components are found in protected coves, on north and east aspects, and at shaded midslope positions. The oak-dominated types are found on the drier, less protected sites; the chestnut oak type is constrained primarily to ridgetops and upper slope positions.

Elevations on the WERF range from 699 to 1,176 m. The topography is dominated by a series of ridges oriented northeast to southwest. Ninety-seven percent of the forested area is made up of 60- to 70-year-old stands of mature hardwoods. However, the majority of the mature stands have been partially harvested at least once in the past decade, and canopy cover is not continuous. The WERF includes three forest types in addition to 140 ha of open or non-forested land. Ninety percent of the forest cover is classified as the sugar maple (*Acer saccharum*)-beech (*Fagus grandifolia*)-yellow birch (*Betula allegheniensis*) SAF type; associated species include white ash (*Fraxinus americana*), American basswood (*Tilia americana*), black cherry (*Prunus serotina*),

yellow-poplar, and northern red oak. The yellow-poplar—white oak—northern red oak type is found on 195 ha of protected coves. The remaining 21 ha are classified as the white oak SAF type; associated species include chestnut oak, scarlet oak (*Quercus coccinea*), black oak, and hickory (*Carya* spp.).

Field Methods

Data were collected in summer 1997. Sample points were established in an approximately square-grid pattern at an intensity of approximately 1 per 2.4 ha. In total, 1,400 points were located on the WVUF and 1,445 points were located on the WERF. The points were georeferenced using a handheld GPS unit and fixed base station that allowed differential correction of the satellite locations. Each point was the center of a 1.72-m-(9.29 m²) radius circular plot on which fecal pellet surveys were conducted (Robinette *et al.* 1958, Van Etten and Bennett 1965). Pellet groups on each of the plots were counted once from June to July on the WVUF and from August to September on the WERF. All pellets were destroyed by crushing. The counts provided baseline data and were not assumed to represent deer activity during any specific season.

Data Analysis

Topographic Variables

We first had to examine the relationships between pellet group densities and possibly confounding variables related to topography. Digital elevation models (DEM's) were available for both experimental forests. The model for the WERF was developed by Westvaco personnel at a resolution of slightly over 15 m. The 30-m resolution USGS DEM was used to describe the topography of the WVUF. We calculated percent slope and aspect in degrees azimuth using the elevation data and the raster-based geographic information system (GIS), IDRISI (Citation). We then standardized the aspect data by subtracting 180 degrees and taking the absolute value of the difference, effectively lumping the data collected on approximately eastern and western aspects (intermediate site quality) while segregating data collected on approximately northern (highest site quality) and southern (lowest site quality) aspects. For each experimental forest, pellet group data were plotted against elevation, slope, and aspect, and relationships were examined.

Variography

Spatial dependence on each experimental forest was quantified with the variogram, a graph that illustrates the relationship between the distance separating pairs of data points (h) and half the average squared deviation of a regionalized variable ($\gamma(h)$). In this case, the variogram

statistic at each given distance h represents half the average squared difference between paired fecal pellet group counts separated by that particular distance (Hohn 1988, Isaaks and Srivastava 1989, Liebhold *et al.* 1991, Rossi *et al.* 1992). The variogram statistic is defined as

$$\gamma(h) = \frac{1}{2n} \sum_{k=1}^{n_h} [z(x_k) - z(x_k + h)]^2$$

where n_h is the number of pairs of cells separated by a distance of h (expressed in meters in this study), $z(x_k)$ is the observed pellet group count at location x_k , and $z(x_k + h)$ is the observed count at a location h meters from x_k . In the absence of spatial dependence, the variogram is constant with distance h . In the presence of strong spatial dependence, the difference between $z(x_k)$ and $z(x_k + h)$ will be relatively small when h is small and will increase with separation distance. At some distance, the difference between counts fails to increase further and the variogram levels off. This distance is referred to as the *range* of the variogram. The value of $\gamma(h)$ at the range is called the *sill*. In general, one would expect the variogram to originate at the origin; however, variograms manifest a non-zero y-intercept when some component of the variability is non-spatial or on a smaller scale than sample spacing.

For each experimental forest, VARIOWIN version 2.2 (Pannatier 1996) was used to calculate the variogram statistic in 120-m lags with a 60-m tolerance to a maximum separation distance of 1,200 m. The first lag included pairs having a separation distance smaller than the tolerance; in other words, all pairs separated by less than 60 m. The few pairs in this lag were retained rather than disregarded. The relationship between pairs separated by more than 1,200 m was not considered. Surface plots of the variogram statistics calculated in the east-west direction versus those calculated in the north-south direction were examined for indications of directionality in the data (figs. 1-2). In the presence of strong directional trends, several individual models are required to accurately describe the spatial dependence in the data. In its absence, a single omnidirectional model is sufficient. In neither data set was there discernible directionality.

Omnidirectional variograms for each forest were plotted using VARIOWIN, and models were fit iteratively by eye (Hohn 1988). Single and nested linear, exponential, gaussian, and spherical model forms were tested for general fit to the shape of the variograms, and the models were fine-tuned by alternately adjusting the *sill* and the *range*. Special care was taken to fit the first few lags accurately, so the final models may or may not have exhibited the best overall goodness of fit. In both cases, the origin was forced through zero.

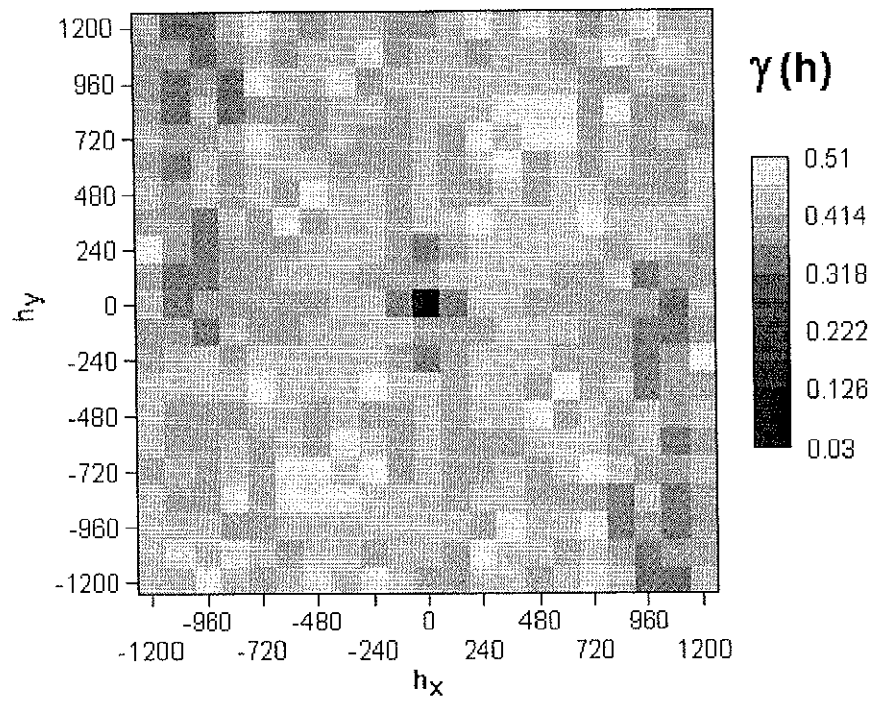


Figure 1.—Variogram surface for the West Virginia University Forest (WVUF).

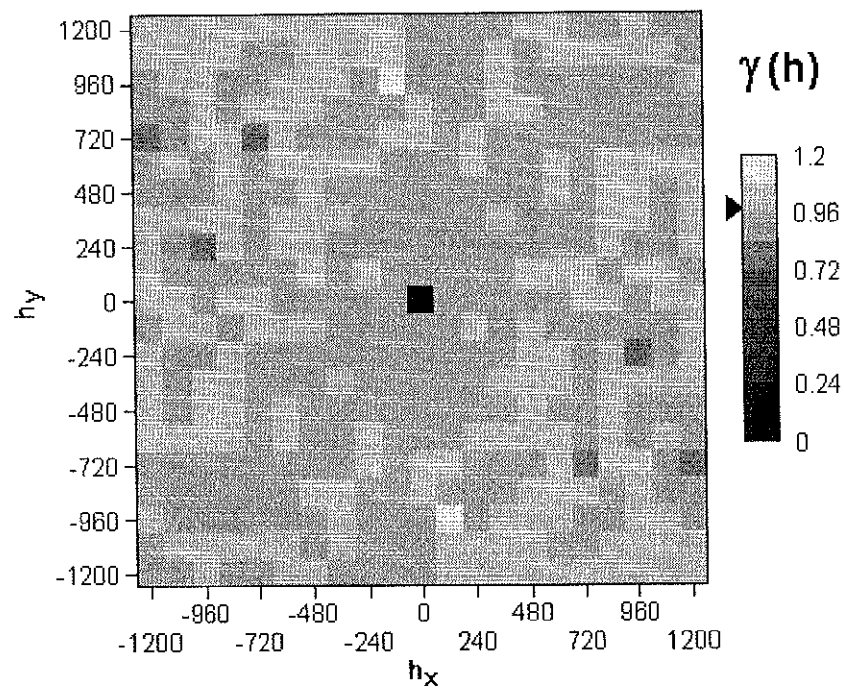


Figure 2.—Variogram surface for the Westvaco Wildlife and Ecosystem Research Forest (WERF).

Kriging

Results of the variogram analysis were used to calculate weights employed in the two-dimensional ordinary point kriging of the pellet count data. Kriged estimates are weighted averages of values at nearby locations

$$z^* = \sum_{j=0}^n w_j \cdot z_j$$

where z^* is the interpolated value being estimated, $z = [z_1, z_2, z_3, \dots, z_n]$ is the vector of values at nearby locations, and $w = [w_1, w_2, w_3, \dots, w_n]$ is the vector of corresponding weights to be used in averaging the values. Because the kriging procedure minimizes the variance of the errors, the weight matrix can be estimated as

$$w = C^{-1} \cdot D$$

where C is the $(n+1)$ by $(n+1)$ covariance matrix and all the z values from nearby samples and D is the $n+1$ vector of covariances of z values between the point being estimated and the nearby samples. The covariances can be computed directly from the variogram as

$$\text{cov}(h) = c - \gamma(h)$$

where c is the variogram sill.

GSLIB version 2.0 was used to krig the data (Deutsch and Journel 1998). Kriged estimates were made at a 30-m resolution and were based on at least 2, but no more than 36, values collected within 500 m of each unsampled location. Estimates made near the boundaries of the experimental forests were necessarily based on fewer samples than those made in the interior.

RESULTS

There were no strong identifiable relationships between the topographic variables and pellet group counts on either of the experimental forests. Aspect may have some effect on the WERF as evidenced by somewhat depressed, but statistically insignificant, pellet group counts on the more southerly aspects. It appears that elevation possibly may be related to counts on the WVUF; however, high pellet group densities at elevations over 600 m were clustered on a portion of the forest that was heavily impacted by overstory mortality in 1990-1991. Higher counts in these areas were likely related to browse availability rather than elevation. Linear regressions through these data were all essentially horizontal with R^2 values less than 0.01. No attempt was made to transform the data.

The variogram surface plots revealed no directional dependence in the WVUF data (fig. 1). Weakly elevated

dependence was suggested among pellet plots oriented in a northeast to northwest direction on the WERF (fig. 2). However, the trend was not strong enough to necessitate the calculation of directional variograms. The majority of the cells in the variogram surface had values of approximately 0.72-0.96; had the values been appreciably lower in the northeast-northwest direction (perhaps in the range of 0.24-0.48), a pair of directional variograms may have improved our ability to model the data.

Omnidirectional variograms and the final fitted models for both forests are shown in figures 3-4. The variogram calculated for the WVUF data was fit with the nested exponential model:

$$\gamma(h) = 0.415 \left[1 - e^{\frac{-3|h|}{231}} \right] + 0.015 \left[1 - e^{\frac{-3|h|}{156}} \right]$$

The omnidirectional variogram for the WERF was fit with the nested model:

$$\gamma(h) = 0.75 \left[1.5 \frac{|h|}{92} - 0.5 \left(\frac{|h|}{92} \right)^3 \right] + 0.20 \left[1 - e^{\frac{-3|h|}{485.48}} \right]$$

if $|h| \leq 92$,

else,

$$\gamma(h) = 0.75 + 0.20 \left[1 - e^{\frac{-3|h|}{485.48}} \right]$$

The first structure in this model is spherical; the second is exponential.

Maps of the kriged estimates are displayed in figures 5-6.

DISCUSSION

The absence of both strong directional trends and strong associations with topographic variables simplifies the modeling process and suggests that differences in pellet group densities are likely related to differences in habitat quality. On both of the study sites, a single omnidirectional model can be used to describe the spatial contagion in the data. In addition, there is no apparent need to incorporate additional independent variables through the use of more complex geostatistical techniques such as cokriging or kriging with external drift (Goovaerts 1997, Deutsch and Journel 1998). This will allow us to monitor the response of deer populations to timber management activities across the study sites without the added complication of confounding variables.

Because the exact location and orientation of the sample plots were not critical in this initial exploratory study, we used temporary locations with the distance between plots paced, rather than measured. This facilitated more rapid data collection but also resulted in less uniformity in the sample design; some plots were installed in closer

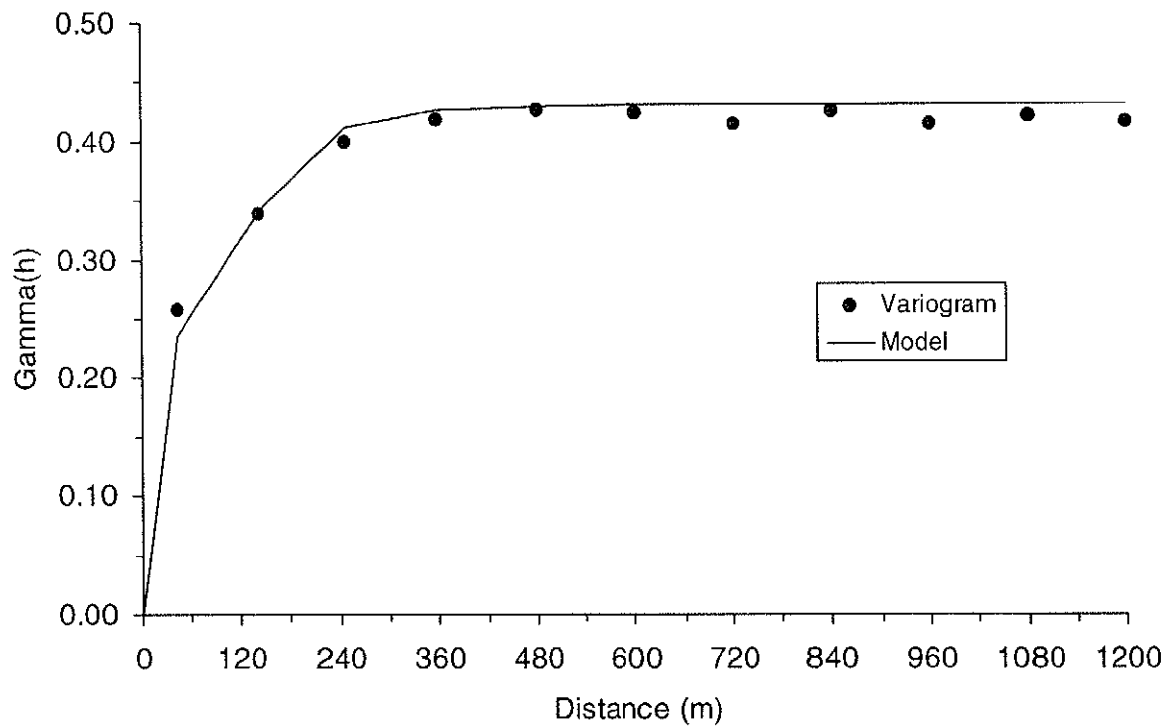


Figure 3.—Variogram and fitted model for the WVUF.

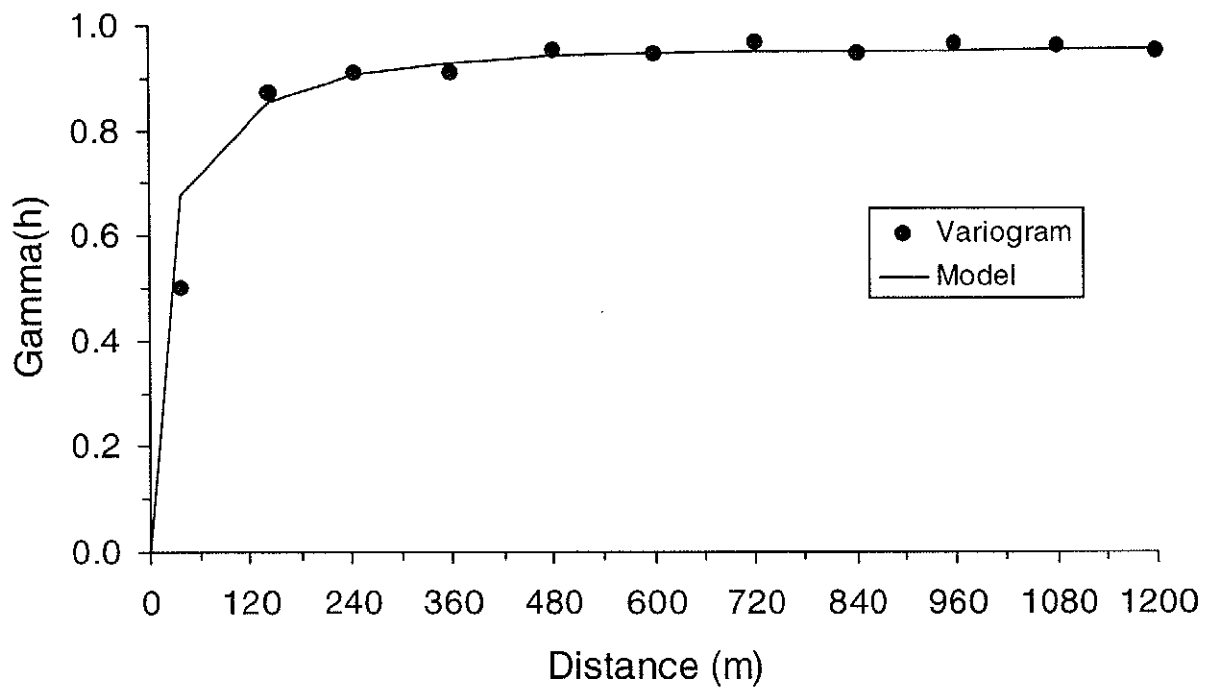


Figure 4.—Variogram and fitted model for the WERF.



Figure 5.—Kriged estimate map for the WYUF.

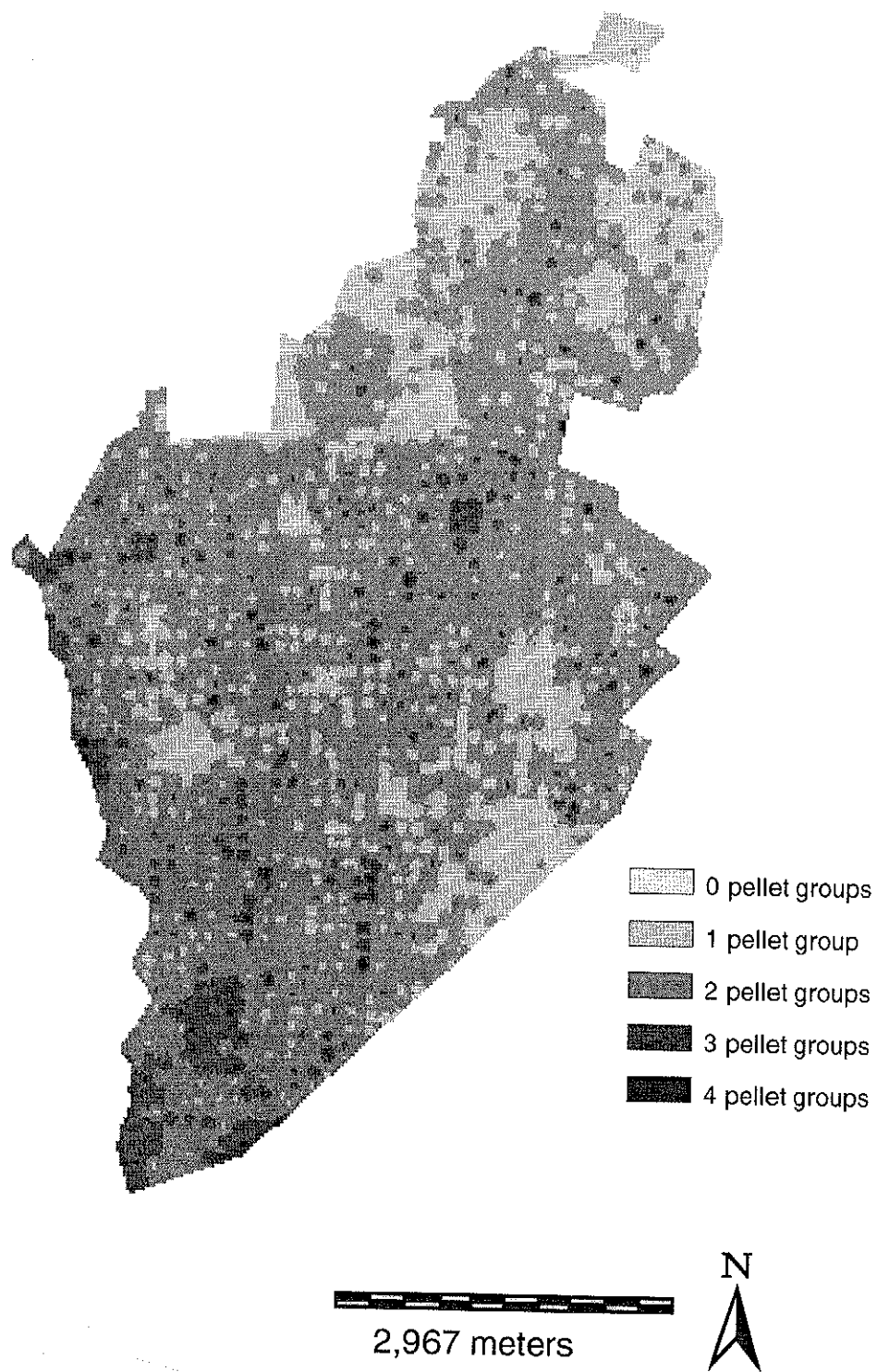


Figure 6.—Kriged estimate map for the WERF.

proximity to adjacent plots than was actually planned. These data could have been omitted; however, we chose to retain them because they provide important information about spatial dependencies in the data at smaller separation distances. The WVUF data included 132 pairs of plots that were separated by an average distance of 42.31 m and 5,832 pairs separated by an average distance of 142.76 m. Numbers of additional pairs ranged from 9,928 at a separation distance of 244.40 m to 37,576 at the maximum separation distance of 1,200.19 m. The WERF data included 78 pairs separated by an average distance of 40.25 m and 5,426 separated by an average distance of 144.03 m. Numbers of pairs ranged from 9,946 at 244.76 m to 39,144 at approximately 1,200 m.

The variogram models for both forests included two nested structures, indicating that on both sites there existed local and regional trends in the data. Both structures used in the construction of the WVUF variogram model were of exponential form. The first had a range of 231 m and sill of 0.415; the second had a range of 156 m and sill of 0.015. The first structure describes the relatively steep increase in variability among pairs of plots separated by an average distance of less than 231 m. The second structure models the gradual increase in variability between separation distances from 231 to 387 m. Ninety-seven percent of the combined sill, or maximum variability, is reached at an average separation distance of 231 m; the remaining 3 percent occurs between 231 and 387 m.

The model used to describe the variogram of the WERF data was more complex. The first structure had a spherical form and describes the steep increase in variability between separation distances of less than 92 m. This structure accounts for 79 percent of the combined sill of 0.95. The second structure, of exponential form, describes a gradual increase in variability to a separation distance of approximately 577 m. It is important to note that the first structure is heavily influenced by the 78 pairs at very close separation distance.

Overall, pellet group counts made on the WERF were more spatially variable than those made on the WVUF. The combined sill of 0.95 for the WERF data was more than double the 0.43 sill for the WVUF data. This was expected given the differences in the sites. The WVUF is relatively uniform and continuous with harvest units clustered along a rudimentary road system. Most of the site has not been actively managed for 80 years, and little of the total area is in early successional stages. In addition, the forest is heavily hunted and deer populations are not excessive (no quantitative estimate of deer densities is available at this time). In contrast, the WERF has been heavily impacted by both partial timber harvest and dispersed regeneration harvests. The habitat is more variable, and more of the total area is covered by young

forest. The area is also heavily bisected by a well-developed road system; however, the WERF is gated and hunting is prohibited. Deer populations are consequently much higher on the WERF; the excessive browsing of woody understory vegetation and paucity of herbaceous vegetation indicate that the site is saturated with deer.

The relative lack of sample data at small separation distances, combined with the strong localized trend in the WERF data, appears in the kriged estimate map as an "egg crate" effect; the overwhelming influence of the most proximal samples caused localized depressions and peaks in the kriged estimates. This problem apparently could be rectified through more intensive sampling. Based on the results of the variography, sampling intensity may have to be more than doubled.

In contrast, the kriged estimates for the WVUF reveal clearly defined areas of heightened deer activity. Less overall variability, a weaker local trend, and a stronger regional trend enabled us to produce an apparently useful predictive map of baseline deer activity patterns. In general, the peaks in estimated pellet counts correspond quite well with known canopy disturbances. For example, peak deer activity occurred in the northeastern lobe of the forest, which was impacted by high overstory mortality in 1990-1991 followed by timber salvage operations. The spike of activity at the tip of the northwestern lobe corresponds with a gas pipeline right-of-way. Peaks in the southeastern corner correspond with recent timber harvest operations.

CONCLUSIONS

In general, pellet group data appear to contain enough spatial contagion to allow the production of estimate maps using two-dimensional ordinary point kriging. Although the estimates have not yet been validated, it appears that spikes in pellet group densities on the WVUF correspond to overstory disturbances and resultant increased availability of woody browse. The results on the WERF were less conclusive and generally indicate that the technique may be less useful in areas of extremely high deer population and variable habitat. However, based on the presence of localized spatial dependence in the small number of samples collected at less than 240 m, it appears that a followup study at higher sampling intensity is warranted before concluding that the technique cannot be used on the WERF or similarly impacted sites.

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