

Scale-dependent proximity of wildlife habitat in a spatially-neutral Bayesian model

Bruce T. Milne¹, Kevin M. Johnston² and Richard T.T. Forman³

Department of Biology, University of New Mexico, Albuquerque, NM 87131, USA; ²Prime Computer Inc., Prime Park, Building 15A, Natick, MA 01760, USA; ³PAES Professor of Landscape Ecology, Graduate School of Design, Harvard University, Cambridge, MA 02138, USA

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Abstract

Organisms may be constrained by the energetic costs incurred while obtaining resources in fragmented landscapes. We used a spatially neutral model of deer wintering habitat to evaluate the effects of landscape fragmentation on the aggregation of deer habitat. The spatially neutral model used Bayesian probabilities to predict where deer wintering areas occurred. The probabilities were conditional on 12 landscape variables measured at 22,750 contiguous 0.4 ha locations. The model predicted deer habitat at each location independently, thereby enabling a comparison of habitat aggregation in observed, simulated, and random distributions of deer habitat. The predictions of the neutral model exhibited greater fragmentation than observed in nature, suggesting that suitable, yet isolated, locations were not visited by deer. The most suitable sites for deer were clumped in the neutral model, regardless of scale. The inclusion of less suitable sites preserved significant aggregation at fine scales but not at broad scales. Species operate at different scales within a landscape, so ecologists, nature reserve designers and natural resource planners may benefit from models that focus on the proximity of habitat sites as a function of both spatial scale and habitat quality.

Introduction

A tenet of landscape ecology is that the juxtaposition of ecosystems or landscape elements regulates the distribution of organisms, resources and energy (Risser *et al.* 1984; Forman and Godron 1986; Urban *et al.* 1987). Certain configurations of resources enable mobile organisms to exploit preferred resources more than average, thus enhancing their growth, reproductive rate or survival (Senft 1986; Senft *et al.* 1987). The implicit assumptions of foraging economics suggest that highly suitable, yet isolated, locations will not be used by organisms if the net gain (e.g., caloric) from visiting them is marginal (see Charnov 1976; Covich 1976). Conversely, locations with less favorable conditions

may be used if they are close to highly suitable locations, thus increasing the aggregation of habitat. The arrangement of resources affects the clustering of organisms on the landscape.

The spatial constraints on the distribution of individuals may be revealed by comparing the observed distribution of organisms with an expected distribution. We considered two alternative expected distributions composed of an equal number of sites. Here, we assume that a map is composed of 'pixels' differing in the landscape variables present. A subset of the pixels, called 'sites', was chosen to represent deer habitat. Sites may be clustered to various degrees depending on the rules used to distinguish sites from other pixels.

The simplest expected distribution is a random

map, wherein sites have equal probabilities, p , of occupying the pixels with $p < 1$, and the number of random sites equals the number of sites on the observed map (Gardner *et al.* 1987). A second, ecologically more appropriate, expected spatial distribution minimizes the effects of foraging economics and historical effects, yet accounts for the environmental variation among pixels. We call this expected distribution a 'spatially neutral model', SNM, because it is generated without hypothesizing spatial factors that regulate the distribution of resources or organisms (see Caswell 1976). Here, the spatially neutral model was generated by estimating the probability that each pixel was used as habitat, given the landscape variables present in each pixel (see Equation 1, below). The SNM differs from a random map because predictions from the SNM are dependent on the observed environmental preferences of the organisms.

Landscape variables that regulate animal habitat may be spatially autocorrelated (Meentemeyer and Box 1987). Thus, the aggregation, or proximity, of sites on a SNM could exceed the proximity of sites on a random map having an equal density of sites; the spatial dependence of the landscape variables used in the SNM results in habitat clustering. Moreover, random maps exhibit non-trivial clustering of sites (Orbach 1986; Gardner *et al.* 1987; Milne 1987), making them worthy of comparison with SNM's, the clustering properties of which are unknown *a priori*. The role of spatial autocorrelation of landscape variables constraining the distribution of habitat may be assessed by comparing the observed distribution to both random maps and SNMs.

Here, we use comparisons between the observed, the SNM, and random maps to test the following hypotheses: (1) spatial autocorrelation of landscape variables produces more clustering in a SNM compared to a uniform random spatial distribution lacking contagion (see Stauffer 1985; Orbach 1986), and (2) a SNM of wildlife habitat exhibits greater fragmentation of predicted sites than the observed distribution. Presumably highly suitable, yet isolated, sites predicted by the SNM may not be visited due to unfavorable foraging economics.

Here, 'habitat' is the place used by organisms

(Whittaker *et al.* 1973). In New Brunswick, Canada, deer wintering habitat was defined as areas occupied by deer herds during consecutive winter months, as determined by aerial surveys and field visits. Wintering habitat was characterized by trampled snow, hoof prints, browsed branches, and excrement obtaining from essentially constant occupancy during the winter. 'Landscape variables' are physical or structural characteristics that may be predictors of habitat.

Knowledge of the precise location of animal populations or resources is difficult to obtain but necessary in many applications (Connelly 1986). Predicting the occupation and utilization of habitat by organisms is complicated by several factors. First, over an arbitrary time scale a landscape may be 'unsaturated' by organisms, leaving many highly suitable locations vacant, and thereby reducing one's ability to differentiate 'habitat' from 'non-habitat'. Second, the habitat is often represented by landscape variables that humans recognize, yet other species may perceive little difference between landscape variables (G. Merriam, personal communication). Third, models using correlations between animal abundance and landscape variables may lack explicit spatial information making it difficult to translate correlational relationships to maps (Shugart and Gilbert 1987). Finally, spatial variation in habitat location may be poorly understood if habitat use is monitored infrequently (Wiens 1981). The success of habitat modeling is affected by animal density, human perceptions, spatial information, and temporal variation.

Here, we present a Bayesian probabilistic model of habitat for white-tailed deer (*Odocoileus virginianus*) living in the Kedgwick River area of New Brunswick, Canada. This model partially circumvents the limitations of using anthropocentric landscape variables by capitalizing on the power of many variables to discriminate suitable habitat from unsuitable locations. The model accounts for the observed habitat density, thereby reducing the chance of predicting habitat where it is not. The resulting maps make predicted habitat locations explicit, thus facilitating planning and management (Milne 1987). Finally, comparisons among observed, random, and neutral habitat maps enable

inferences to be made about the effect of landscape patterning on the clustering of habitat,

Methods

Study area

The study site is an isolated; forested area along a 20 km stretch of the Kedgwick River, between Kedgwick Forks and Rapids Depot, 90 km north-east of Edmundston, New Brunswick, Canada. The ~ 5-km width of the study site includes portions of the Kedgwick watershed. The steep slopes have prevented all but minor logging. A forest road paralleling the river to the south, a logging camp at Rapids Depot, and a seasonal range camp are the only current signs of human use. The Kedgwick River is the major hydrological feature of the study area.

The summer mean monthly temperature is 14.6°C with mean rainfall of 735 mm. Winter temperatures average -7.5°C, with 378 mm of precipitation. Glacial features include steep, narrow, valleys composed of tills and thin, stony tills. Alluvial sediments and sand and gravel floodplains are found in the lowlands.

Over 70% of the vegetation of the study area consists of spruce (*Picea rubens*) and fir (*Abies balsamea*). Conifers include the pines *Pinus resinosa*, *P. banksiana*, and *P. strobus* and small amounts of larch (*Larix laricina*), hemlock (*Tsuga canadensis*), and cedar (*Thuja occidentalis*). Hardwoods, present in dense patches, account for 18% of the total stem density. Low timber harvesting rates and low amounts of disturbance have apparently predisposed the vegetation to spruce budworm damage over 10% of the site, thereby increasing fuel loads.

Wildlife is abundant, including black bear, moose, otter, beaver and mink. White-tailed deer, which are at their northern range limit in the Kedgwick basin, and salmon are protected by governmental conservation programs.

The data base and software

Several Geographic Information Systems (GIS), ac-

companied by numerous utility programs were used for creating the data base, performing analyses, and presenting results. All digitizing and data base creation were accomplished using two vector-based GIS's: (1) ARC/INFO, developed by Environmental Systems Research Institute (ESRI) and (2) Odyssey, developed by the Harvard University Laboratory for Computer Graphics. A third GIS, the raster-based Map Analysis Package (MAP) developed by Dana Tomlin at Yale and Harvard Universities, was used for preliminary analyses and sampling, although custom routines were written for constructing the Bayesian habitat model. Other programs from the Harvard Computer Graphics Laboratory included: **Reduce**, for lessening the number of component parts of the raster neighborhood; **Newold**, for changing files from binary to ASCII; and **Imagomundi**, for generating shaded relief maps from a raster data map.

The data base included 25 base overlays. Topography was derived from white-line orthophotographs and digitized at a scale of 1: 10,000. The individual overlays for deer wintering habitat, government designated areas providing protection, major and minor forest roads, and primary, secondary, and tertiary hydrological features were input at 1:20,000. Soils and R.C. Gauthier's glacial deposit classification map were input at 1:250,000 and 1: 100,000 scale, respectively. The remaining layers, including immature spruce densities, mature spruce, overmature spruce, immature fir, mature fir, overmature fir, pine, other softwoods (i.e., larch, cedar, and hemlock), hardwoods, dead softwood, windthrow-affected areas, budworm-affected areas, and crown-closure density, were derived from aerial photographs at 1:30,000 scale.

Data in the analyses presented here were coded in ~ 0.41 ha 'pixels' representing 37 landscape variables. Variables were grouped into 'map layers' such that related, mutually exclusive thematic landscape variables occurred on the same map layer: For example, the 'pine' layer included pixels representing pine density ranging from 10 to 100% in increments of 10 percentage points: each percentage class represented one landscape variable. A separate map layer contained a binary representation of deer wintering habitat, *i.e.*, the pixels contained 0 or 1 to

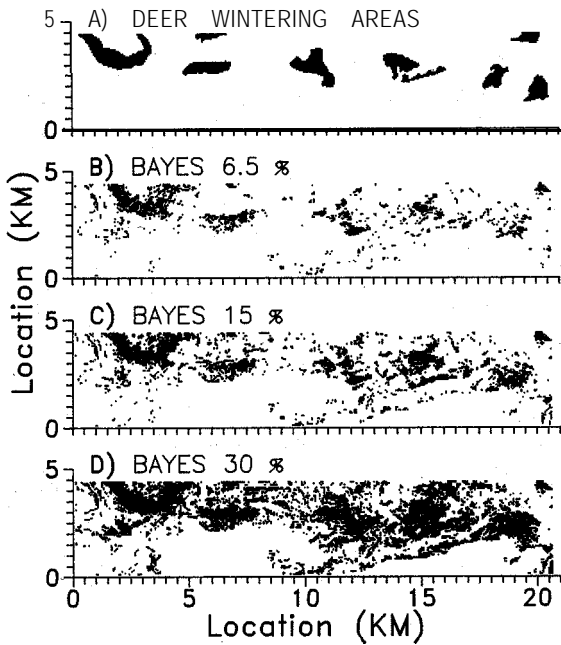


Fig. 1. Habitat maps for white tailed deer in the Kedgwick River area of New Brunswick, Canada. (A) known locations of wintering areas. (B), (C), and (D) the most likely 6.5, 15, and 30% of the sites for deer wintering areas, respectively, as predicted using the Bayesian habitat model.

represent non-deer habitat and deer habitat, respectively (Fig. 1a).

Pixels were aggregated into square 'cells' to conduct analyses at several scales. For studies of habitat proximity, or aggregation, cell sizes included 16, 64, 196, 324, and 484 pixels representing approximately 6.5, 25.9, 79.3, 131.1, and 195.9 ha, respectively. Other cell sizes and configurations (described below) were used in a multivariate analysis of variance and for studying the effects of neighboring cells on the Bayesian habitat model.

Habitat modeling

Development of the habitat model involved two steps. First, we tested the hypothesis that the landscape data were useful for discriminating deer habitat from non-deer habitat. The second step involved creating a Bayesian model predicting the probability of deer being present or absent given the states of landscape variables at each pixel within the

study region.

A stratified random sample was used to test whether the landscape variables were useful for modeling deer habitat. We randomly selected 220 independent sampling cells within the areas known to be used as wintering areas and within 220 areas without wintering areas. The frequencies of the 37 landscape variables were determined for each cell (3×3 pixels, ~ 3.6 ha), providing counts ranging from 0 to 9. The landscape variables were treated as dependent variables in a one-way classification multivariate analysis of variance (MANOVA) to test for habitat differences between wintering areas and unused areas.

Computational requirements for the Bayesian model were reduced by identifying variables that contributed to the differences between the two habitat states. Variables were chosen if they significantly reduced the unexplained variance in separate one-way analyses of variance. Examples described below include three soil types, various percentages of canopy closure, and relative density of spruce (*Picea rubens*).

The Bayesian model

Construction of the Bayesian model required maps of 12 landscape variables such as forest composition and soil types (Table 1). Each pixel on the landscape was described by a vector, x , containing a list of the variables present. Then, the probability of each 'state' of wildlife populations, w , at each pixel was calculated, conditional on the vector of landscape variables present. Here, the states included 'deer habitat present' and 'deer habitat absent'. According to Bayes' formula.

$$P(w_j | x) = \frac{p(x | w_j) P(w_j)}{p(x)} \quad (1)$$

where

$$p(x) = \sum_{j=1}^n p(x | w_j) P(w_j)$$

Here, $p(x | w_j)$ is the state-conditional probability density function for x , $p(w_j)$ is the **a priori** proba-

Table 1. Landscape variables selected to generate the Bayesian probabilities for predicting the presence of deer wintering areas.

The percentages of variance explained by univariate models (R^2) indicate the role of individual variables in discriminating deer habitat from non-habitat. Mean area covered by each variable within 220 \sim 3.6 ha sampling cells is given, followed by the standard deviation in parentheses.

Variable	Area covered (ha)		R^2
	Deer absent	Deer present	
Soil types:			
Thibalt, 1 m deep loam	0.98 (1.54)	2.28 (1.67)	13.98
Thibalt, 2 m deep loam	0.54 (1.25)	0.02 (0.24)	7.95
McGee, 1 m deep loam	1.58 (1.74)	0.59 (1.30)	9.27
Canopy closure:			
30%	0.36 (0.72)	0.17 (0.47)	2.27
70%	1.54 (1.31)	2.00 (1.39)	2.80
90%	1.13 (1.33)	0.75 (1.06)	2.39
Hardwood composition:			
20%	0.56 (0.98)	0.21 (0.49)	4.70
'Immature' Picea:			
10%	0.39 (0.78)	0.16 (0.44)	3.19
20%	1.15 (1.32)	0.81 (1.16)	1.83
'Overmature' Picea:			
10%	0.96 (1.28)	1.60 (1.31)	5.73
20%	0.52 (0.99)	0.26 (0.72)	2.23
Miscellaneous softwood:			
30%	0.05 (0.34)	0.23 (0.63)	3.00

bility of state w_j , and $P(w_j | \mathbf{x})$ is the **a posteriori** probability of each state, given the set of landscape variables present (Davis 1986). The predicted state of each pixel is independent of the probabilities for other pixels. This independence constitutes the spatial neutrality of the model.

When equation (1) is used as a discriminant function each pixel is assigned to a state according to 'Bayes' rule'. Bayes' rule assigns a pixel to whichever state has the highest **a posteriori** probability given the vector of landscape variables present. We explored the spatial consequences of other decision rules by assigning pixels to the 'deer habitat present' state if the **a posteriori** probability was greater than an arbitrary 'threshold' value. Threshold values were chosen such that sufficient pixels

were designated as 'deer habitat' to provide maps having 6.5, 15, and 30% aerial coverage of sites; less probable sites were included to increase total aerial coverage. Aerial coverage was the percentage of the total number of pixels occupied by deer habitat sites. Here, 'sites' is used to indicate pixels containing deer habitat, be they observed, random, or predicted by Equation (1). The coverages of 6.5, 15, and 30% bracketed the aerial coverage of observed sites, **i.e.**, 9% aerial coverage (Fig. 1a). The coverages represented possible changes in habitat coverage through time, or differences in maps constructed by habitat managers using different criteria.

Additional investigations included (1) studies of the aggregation, or proximity, of predicted sites at several scales, and (2) the effect of including 'neighborhood' conditions in calculations of the Bayesian probabilities. Proximity was assessed at a variety of spatial scales (*i.e.*, using five cell sizes) with the following measure:

$$\Pr(p_s \geq p_g) \quad (2)$$

which is the probability that the aerial coverage of wildlife habitat, p_s , at a given spatial scale (*i.e.*, cell size) exceeds the 'global' coverage, p_g , on the entire map (*i.e.*, $p_g = 6.5, 15, \text{ and } 30\%$). Low values of the proximity index indicate that sites are concentrated in clusters. Proximity was calculated using cell sizes of $6.5, 25.9, 79.3, 131.1, \text{ and } 195.9 \text{ ha}$. Comparisons of the proximity of sites on Bayesian maps to the proximity on random maps are sensitive to the value of p_g and to the extent of the map, **i.e.**, the number of pixels along each edge of the map (Stauffer 1985; Gardner *et al.* 1987). A frequency distribution of $\Pr(p_s \geq p_g)$ values was generated for 3 1-74 random maps (70 by 325 pixels each) having aerial coverages of 6.5, 15, or 30%. Separate distributions were calculated for each of the five cell sizes. The values of $\Pr(p_s \geq p_g)$ from the three Bayesian maps were then subtracted from the mean values obtained from the replicated analyses of random maps. The numerical differences between the proximity probabilities of Bayesian maps and the mean proximity values of random maps were used to test whether the proximity observed -on Bayesian maps could have occurred at

random, *i.e.*, the null hypothesis was rejected when the observed deviation from the random mean was more extreme than 99% of the random observations, one-tailed test.

Neighborhood effects were also incorporated in the model to determine whether predictions of the Bayesian model could be made to resemble the observed contagion of deer habitat sites, assuming that deer evaluate their habitat on a scale >0.4 ha. Neighborhood effects were measured by constructing a new vector for each pixel. This new vector measured the frequency of each landscape variable (listed in Table 1) in the surrounding 8 pixels (~ 3.2 ha). Used in their raw state and in conjunction with the original 2390 possible site vectors, the number of unique combinations of landscape variables at each pixel would have been impracticably large (*i.e.*, $2390^9 = 2.5 \times 10^{30}$ combinations!). Consequently, cluster analysis (*i.e.*, Fastclust, Helwig and Council 1979) was used to classify the neighborhood vectors into two classes. Each pixel was assigned the cluster value of the surrounding neighborhood, and this value was combined with the original x vector for recalculation of the Bayesian model (Equation 1).

Variation in the density of predicted sites (*i.e.*, number of sites/cell area), as a function of the scale at which measurements were made, was evaluated at scales ranging from 6.5 to 195.9 ha (see above). A full-order 3-way classification ANOVA was used to test for the effects of (a) scale; (b) total aerial coverage of deer habitat (*i.e.*, 6.5, 15, and 30%), and (c) neighborhood vs. non-neighborhood versions of the Bayesian model.

In summary, the probability that the Bayesian habitat maps exhibited contagion equal to that expected at random was calculated at five scales. Deviations of the predicted habitat from the observed map were considered indicative of the role of spatial effects or possibly historical effects regulating the distribution of organisms. Finally, the model was adapted to incorporate 'neighborhood' effects of the surrounding cells.

Results

Deer wintering areas were relatively simple in shape

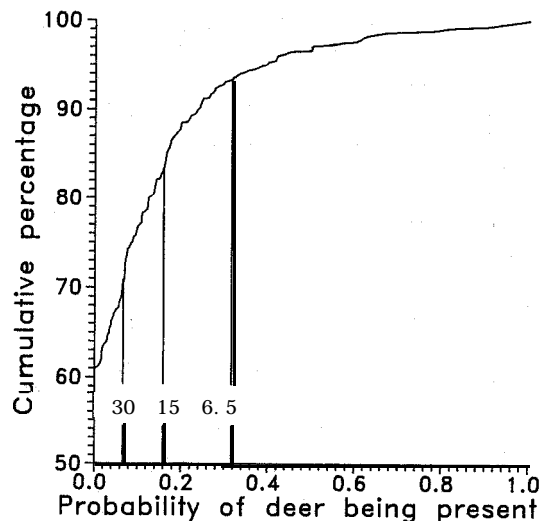


Fig. 2. Cumulative distribution of the Bayesian probabilities that 0.4 ha sites in the New Brunswick, Canada landscape contain deer wintering areas. Probabilities were based on Equation (1) without information regarding neighborhood characteristics. Vertical lines indicate the probability thresholds used to select groups of sites covering 6.5, 15, and 30% of the landscape.

and compact (Fig. 1a). The multivariate analysis of variance demonstrated a significant difference in landscape variables between deer habitat and non-deer pixels for data measured within 3.6 ha cells (Wilkes lambda = 0.612, $F(56,383) = 4.33$, $p = 0.0001$). Computational constraints in constructing the Bayesian model limited our choice of independent landscape variables to those that reduced the unexplained variance by at least 1% (Table 1). These 12 variables exhibited modest differences between cells used vs. unused by deer. However, the combined effect, as tested by MANOVA, was highly significant, thus justifying use of the data for building a multivariate Bayesian model of habitat.

The Bayesian models

Several versions of the Bayesian distribution were made for comparison with the observed distribution (Fig. 1a). First, the most conservative predictions were those made using 'Bayes' Rule', which predicts that deer will be present at sites where the probability of deer being present, given the condi-

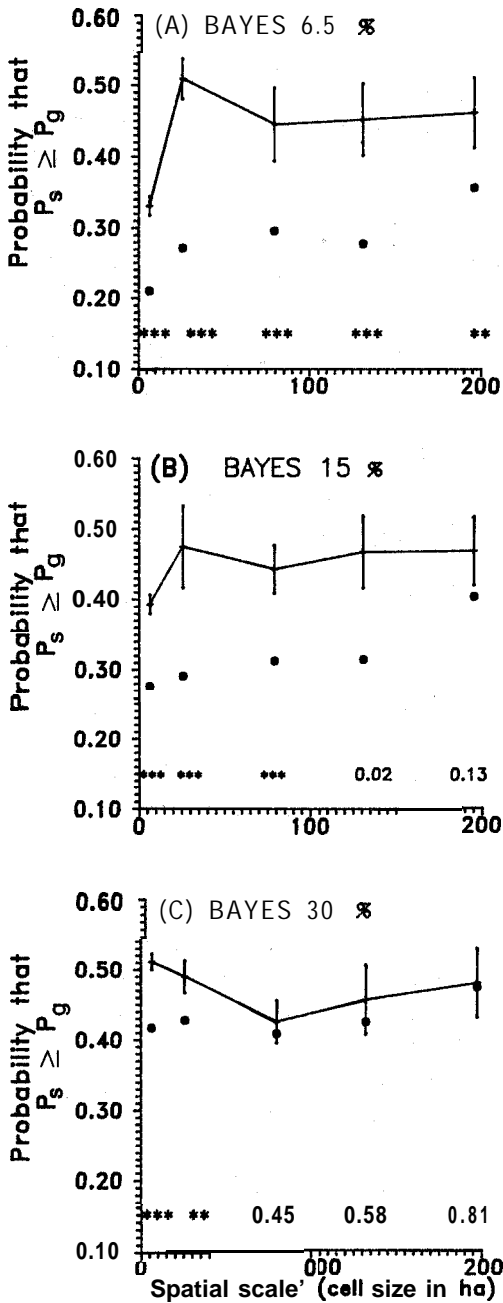


Fig. 3. Proximity analysis of random maps and deer wintering sites predicted from the spatially neutral Bayesian model. The probability that the portion of local coverage of wintering sites (p_s) exceeded the percentage for the entire map (p_g) is plotted versus the area of the cell used to make the measurement. (A), (B), and (C) are for maps having 6.5, 15, and 30% coverage of sites, respectively. Solid dots represent values that were calculated from the Bayesian maps (see Fig. 1). The solid curve connects means for random maps; vertical lines represent one standard

error of the mean. The decimal number beneath some solid points is the probability that the observed value obtained from the Bayesian map belonged to the random distribution. Significant deviations between the proximity of sites measured on Bayesian maps vs. random maps are indicated by asterisks; ** = $p < .01$, *** = $p < .0001$; one tailed test.

error of the mean. The decimal number beneath some solid points is the probability that the observed value obtained from the Bayesian map belonged to the random distribution. Significant deviations between the proximity of sites measured on Bayesian maps vs. random maps are indicated by asterisks; ** = $p < .01$, *** = $p < .0001$; one tailed test.

To compare the spatially neutral Bayesian model with the actual deer habitat, the cumulative probability distributions for the probabilities of deer being present were partitioned (Fig. 2) to provide maps showing the most likely 6.5, 15, and 30% of the sites (Fig. 1b-d). Successively dense maps contained all of the sites of sparser maps, plus additional sites with lower probabilities of deer habitat. As successively dense maps were examined (i.e., higher p_g), the predicted sites 'radiated' outwards from centers of distribution. This spreading outwards from cores of distribution reflected the spatial autocorrelation of sites that were suitable for deer.

Analysis of variance of the density of predicted sites revealed significant effects of both the scale of measurement and the aerial coverage of sites (i.e., 6.5, 15, and 30%) on the map (arcsine-square root transformed density; scale effect, $F(4,974) = 8.94$, $p = 0.0001$; coverage effect, $F(2,974) = 145.44$, $p = 0.0001$). No significant difference was found between the two neighborhood versions of the model, nor were any interaction effects significant. Both the scale of measurement and the threshold used to make the maps affected the density of predicted sites.

Analysis of the proximity of predicted habitat sites using Equation (2) indicated an interaction between the scale at which proximity was measured and the threshold used to create the habitat map. For example, the Bayesian maps with 6.5 and 15% aerial coverage had sites aggregated more than expected on random maps at all or most scales (Fig. 3a, b). In contrast, the habitat map with 30% coverage (Fig. 1d) exhibited aggregations that could be expected at random at the three broadest scales

error of the mean. The decimal number beneath some solid points is the probability that the observed value obtained from the Bayesian map belonged to the random distribution. Significant deviations between the proximity of sites measured on Bayesian maps vs. random maps are indicated by asterisks; ** = $p < .01$, *** = $p < .0001$; one tailed test.

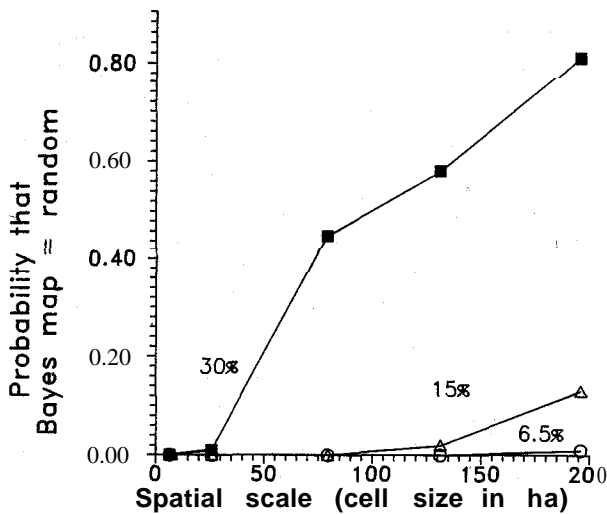


Fig. 4. The dependence between site proximity and the scale of measurement. The probability that sites were equally aggregated in Bayesian habitat models and random maps is plotted for several scales.

examined (Fig. 3c). Thus, the proximity of sites varied with scale, and this response was affected by the threshold chosen to create the map.

The interaction between scale and aerial coverage of sites was summarized by comparing the probabilities of rejecting the null hypothesis (i.e., proximity on the Bayesian maps equals that on random maps). With increases in p , a correlation emerged between the proximity of suitable sites and the scale at which observations were made (Fig. 4). The probability of rejecting the null hypothesis was greatest for the least discriminating map (Fig. 3c); less suitable sites combined with the most suitable sites were significantly aggregated at fine scales and distributed randomly at broad scales.

Discussion

The spatially neutral Bayesian model revealed that the proximity of predicted habitat sites varied with both the spatial scale at which measurements were made and with the probability threshold used to predict deer habitat (Figs 3 and 4). We may expect the New Brunswick, Canada landscape to appear differently to each species, given that species function at different scales (Brown 1981; Brown and

Maurer 1987) and have different resource requirements. The rate at which the slopes of the curves in Fig. 4 change with the addition of less suitable sites to the map may indicate how sensitive a species is to the spatial patterning of landscape variables or resources. All the curves would be nearly flat in landscapes with random distributions of resources. With significant clustering of resources, the slopes would change rapidly as marginal habitat sites were added. The spatial autocorrelation of preferred environments promotes clumping of habitat sites. The addition of marginal sites increased habitat fragmentation in the spatially neutral model.

The scaling behavior exhibited in Fig. 4 may vary with species' habitat preferences. Habitat models for generalist species showing little habitat specificity are more likely to have flatter curves than those for specialists which should be more sensitive to the clustering of resources. It is unknown how the response to variables observed at different scales depends on other ecological characteristics related to population density, such as body mass (see Brown 1981; Peters 1983). However, the sensitivity of many species to scale could be valuable for predicting the assemblage of communities within landscapes differing in resource distribution. Prediction of community assemblages may require both specifying the spatial distribution of landscape variables and determining species responses to the variables. The effect of scale will depend on a species' ability to detect resources and on the distribution of landscape variables.

Temporal changes in habitat proximity may reflect variation in resource abundance. Habitat may expand when resources are abundant everywhere, resulting in decreased aggregation of habitat at most scales (Fig. 3c). Thus, variation in habitat clustering with scale may be indicative of the degree to which constraints are operative (see Milne 1988a).

The effect of scale on proximity (Fig. 4) is relevant to the design of landscapes for wildlife management. Some management schemes prescribe maximizing habitat diversity within 40 ha areas (e.g., Evans 1974) contained within much larger landscapes. If such a policy were carried out in New Brunswick, Canada, the proximity of habitat in the

managed landscape would be random at scales greater than 40 ha (*cf.* Fig. 4). Maximizing habitat diversity at an arbitrary scale could alter the patterning of habitat that typically varies with scale.

Often, ecologists have focused on 'the appropriate scale' for analysis. Such analyses (e.g., Kershaw 1960; Greigh-Smith 1964) may examine the variance measured at several scales, or in 'blocks' of different sizes. The appropriate scale for comparison among blocks is based on the scale that maximizes the variance among blocks, presumably because important ecological factors vary at that scale. Consequently, complex spatial interference patterns among population patterns occur at the community level if the population densities of species vary at different scales (Noy-Meir and Anderson 1973). Thus, attempts to find 'the appropriate scale' at the community level are confounded if the densities of populations, or resources, differ at various scales.

Alternatively, spatial analysis may focus on the variation in resource abundance, community composition, or habitat proximity at several scales simultaneously (Burrough 1983; Palmer 1988, Fig. 4). Viewing ecological patterns at many scales allows the 'patterns' to be described by parameters, such as fractal dimensions, that are constant across a finite range of scales (Mandelbrot 1983; Milne 1988b). An advantage of multi-scale analysis is that direct comparisons are possible between studies conducted at various scales because the results are independent of the sampling scale (see Milne 1987). Also, the factors regulating populations may change through time, suggesting that the appropriate block size may change as well. Long-term monitoring conducted at only one scale may confound the observer's ability to discern changing controlling factors. In multi-scale analysis, changes in the block size at which variance is maximal are reflected in a changing fractal dimension of the pattern (e.g., Burrough 1981). Thus, multi-scale analysis buffers the observer from misinterpreting ecological relationships occurring first at one scale and then at another.

In developing a habitat model with greater predictive power, conditional probabilities could be used to locate habitat sites in a clumped fashion.

Such an approach would increase the probability of a site being classified as 'habitat' if it were surrounded by sites with high *aposteriori* probabilities from Equation (1). Deviations between this model and the species distribution might reveal more subtle effects of anisotropism stemming from topography, for example, thereby motivating a further refinement of the model. Thus, the neutral model would evolve towards complexity, albeit in a parsimonious fashion.

Likewise, the deviation of a model from a simple expectation (Fig. 4) is indicative of higher-order spatial effects in the landscape. Had the New Brunswick study area been highly repetitious at the scale of ~ 10 ha, we would not have expected the differences in proximity observed among the various maps (Fig. 4). Rather, the 'gyres' apparent in Fig. 1d represent broad-scale features that imposed the interaction between scale and threshold found in the proximity analysis. Departures from expectation are indicative of non-random landscape characteristics (Gardner *et al.* 1987).

In summary, measurements of landscape complexity are sensitive to the extent of the area measured and to the overall aerial coverage of the landscape feature of interest. The sensitivity of species to these same parameters may be used to manage landscapes, and to understand the assembly of species in regions differing in landscape complexity.

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