

Distribution and density of moose in relation to landscape characteristics: effects of scale¹

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Abstract: We analyzed the relation between early winter distribution and density of female moose (*Alces alces* L.) and habitat heterogeneity in interior Alaska. We tested for effects of vegetation type, topography, distance to rivers and towns, occurrence and timing of fire, and landscape metrics. A spatial linear model was used to analyze effects of independent variables organized at multiple scales. Because densities of moose vary widely as a result of differences in management and other factors, a spatial response surface of the log of moose density was fit to remove large-scale effects. The analysis revealed that the densest populations of moose occurred closer to towns, at moderate elevations, near rivers, and in areas where fire occurred between 11 and 30 years ago. Furthermore, moose tended to occur in areas with large compact patches of varied habitat and avoided variable terrain and nonvegetated areas. Relationships of most variables with moose density occurred at or below 34 km², suggesting that moose respond to environmental variables within a few kilometres of their location. The spatial model of density of moose developed in this study represents an important application for effective monitoring and management of moose in the boreal forest.

Résumé : Les auteurs ont analysé les relations entre la répartition et la densité de femelles d'orignal (*Alces alces* L.) en début d'hiver et l'hétérogénéité de l'habitat en Alaska continentale. Ils ont évalué les effets du type de végétation, de la topographie, de la distance par rapport aux rivières et aux villes, de l'occurrence et de l'année des feux et des métriques du paysage. Un modèle linéaire à contrainte spatiale fut utilisé pour analyser les effets des variables indépendantes selon différentes échelles. Étant donné que la densité d'originaux varie beaucoup en fonction de l'aménagement et d'autres facteurs, une surface de réponse spatiale du logarithme de la densité d'originaux fut ajustée pour enlever les effets à grande échelle. Les analyses ont révélé que les populations les plus denses d'originaux se trouvaient près des villes, à des altitudes modérées, près des rivières et dans les endroits où il y a eu un feu 11–30 ans auparavant. De plus, les originaux avaient tendance à occuper des zones caractérisées par de vastes parcelles d'habitats denses et diversifiés et ils évitaient les terrains raboteux ainsi que les aires dénudées de végétation. Les relations observées entre la plupart des variables et la densité d'originaux l'ont été à une échelle de 34 km² ou moins, ce qui indique que l'orignal réagit à des variables environnementales dans un rayon de quelques kilomètres du lieu où il se trouve. Le modèle à contrainte spatiale de la densité d'originaux développé dans cette étude constitue un outil intéressant pour faire un suivi et un aménagement efficaces de l'orignal en forêt boréale.

[Traduit par la Rédaction]

Introduction

Landscape heterogeneity is known to be an important component of ecosystem dynamics and processes (Turner 1989; Turner and Gardner 1991). Heterogeneity affects predator–prey dynamics (Bowman and Harris 1980; Pierce et al. 2000),

competition among species (Pacala and Roughgarden 1982), population and metapopulation processes (Stenseth 1980; Dempster and Pollard 1986; Dunning et al. 1992; Henein et al. 1998) and, thereby, conservation biology (With 1997). Spatial heterogeneity has been implicated in the home-range dynamics of mule deer (*Odocoileus hemionus*; Kie et al.

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2002) and habitat selection of elk (*Cervus elaphus*; Boyce et al. 2003). The vagility of large mammals makes them an ideal model for studying effects of landscape heterogeneity on ecological processes because they integrate effects of landscape structure over large areas (Bowyer et al. 1997; Kie et al. 2002). Moreover, large herbivores are capable of driving ecosystem processes (Hobbs 1996; Bowyer et al. 1997; Kie et al. 2003), including trajectories of vegetation succession (Pastor et al. 1993; McLaren and Peterson 1994) and nutrient cycling (McNaughton 1984; Ruess and McNaughton 1987; Frank and McNaughton 1993; Molvar et al. 1993). Effects of large herbivores on ecosystems can have implications for biodiversity; hence, a better understanding of factors underpinning the distribution of large herbivorous mammals is necessary for the management and conservation of ecosystems.

Many ecological patterns and processes are thought to be scale dependent (Weins 1989; Kotliar and Wiens 1990; Schneider 1994; Gardner 1998; Levin and Pacala 1997). Effects of scale on habitat use and selection have been investigated extensively (Morris 1987; O'Neill et al. 1988; Powell 1994; Rachlow and Bowyer 1998). Scale may have profound effects on life-history strategies of large mammals (Bowyer et al. 1996, 2002), including the manner in which these organisms distribute themselves across the landscape (Kie et al. 2002; Boyce et al. 2003). Indeed, Kie et al. (2002) reported that home-range sizes in mule deer are dependent on habitat features located far outside the home-range boundaries. Consequently, an understanding of the effects of habitat heterogeneity on the distribution of animals is not independent of the scale at which they are measured nor the scale at which the animal perceives them.

We selected moose (*Alces alces* L.) in interior Alaska, USA, to study the effects of landscape heterogeneity and scale on the density of this large herbivore. Moose traverse large expanses of boreal forest with few anthropogenic disturbances, and they respond markedly to natural perturbations of their environment, especially fire (Peek 1974; Wolff 1978; Bangs and Bailey 1980; Loranger et al. 1991; Weixelman et al. 1998). Moose are also an essential cultural and economic resource for subsistence and sport hunters (Reeves and McCabe 1998) and as such are a primary focus of resource management agencies in northern regions.

Fire is the major disturbance in the boreal forest that contributes to habitat heterogeneity, but how the age and juxtaposition of fire affects the density and distribution of moose on a landscape scale is poorly understood. Moose respond strongly to successional changes in vegetation following fire (Schwartz and Franzmann 1989; Loranger et al. 1991; Weixelman et al. 1998). In the boreal forests of interior Alaska, MacCracken and Viereck (1990) noted a marked increase in browse production (mostly aspen, *Populus tremuloides*) 5 years after burning. Although we expect an increase in forage production by willows (*Salix* spp.) following fire (Wolff 1978), the duration of the increase is unknown. Gasaway et al. (1989) noted that in interior Alaska, moose without prefire experience in an area do not respond to a fire, even after 5 years. Likewise, Jandt (1992) reported that fire has a minor influence on habitat selection by moose in western interior Alaska, an area that has increased riparian habitat and a lower frequency of fire than does eastern interior Alaska (Calef et al. 2005).

Resolving the relationship of moose density to habitat characteristics and scale has been hampered by extreme variation in density of this large herbivore across sufficiently large areas. Some moose populations are held at extremely low density by a suite of large mammalian carnivores (Gasaway et al. 1992; Bowyer et al. 1998), whereas others have attained relatively high densities (Keech et al. 2000). Herein, we overcome that problem by removing the large-scale pattern in moose density among populations while maintaining variability within populations so that we might evaluate the role of habitat heterogeneity and spatial scale on moose density. Specifically, we tested for effects of vegetation type, topography, distance to rivers and towns, the occurrence and timing of fire, and a suite of landscape characteristics related to heterogeneity including patch, edge, shape, proximity, diversity, and contagion metrics while progressively extending the size of our sampling units to encompass larger landscape domains (sensu Kie et al. 2002). Our purpose was to understand how variation in landscape and habitat features, especially fire, affect the density of moose and to gain insights into the scale at which moose respond to landscape and habitat features.

Materials and methods

Overview

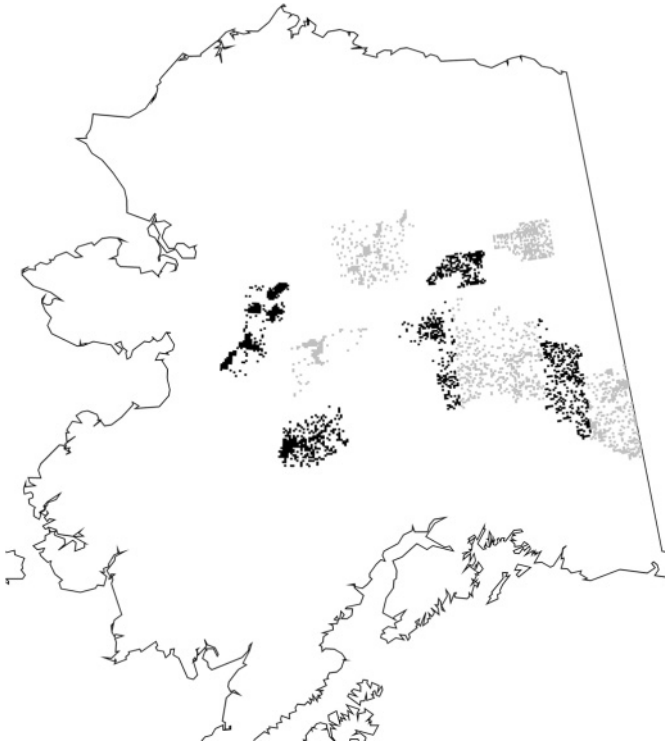
To evaluate the effects of fire on density and distribution of moose across interior Alaska we related survey data collected by the Alaska Department of Fish and Game, the US Fish and Wildlife Service, and other government agencies to various spatial data. The methods are described in Ver Hoef (2001, 2002). Moose surveys were conducted in autumn following the mating season (rut) and after sufficient snowfall made moose more visible (from late October to early December from 1998 to 2001). Each survey area was stratified into low and high population densities of moose, and a random selection of units was sampled from each of those strata. Sample units were 2' latitude × 5' longitude and approximately 15 km². In each sample unit, all moose were counted and classified into sex classes and age-classes of young (<1 year old), yearling, adult (≥2 years old) male, or adult female. Because the female portion of the population is the most stable and reflects the autumn distribution of males (Miquelle et al. 1992), we only analyzed counts of female moose in sample units. Counts of female moose were log transformed to meet assumptions of normality. In instances where a sample unit was observed over multiple years, we computed the mean of the log-transformed count for that unit, but also recorded the sample size for that mean, which was used later in analyses. In all, we used data on 2628 unique sample units, some of which were measured multiple times (Fig. 1).

Our analysis uses a geostatistical spatial model based on points and distances, so we determined the latitude and longitude from the center of each sample unit. Then, to make x- and y-coordinates comparable, we converted latitude and longitude to Universal Transverse Mercator (UTM) coordinates.

Explanatory variables

We overlaid data from moose surveys on a variety of spatial data using the geographic information system ArcView

Fig. 1. Location of the 2628 unique sample units used in this study to analyze the distribution of female moose density in interior Alaska, USA (1998–2001). Different shades indicate the 10 groupings used for the restricted maximum likelihood (REML) estimation of autocorrelation parameters.



3.2a (Table 1). We conducted analyses at multiple scales to determine whether moose respond to their environment on a particular scale. The initial sampling region was defined as a circle with an area of 15 km² (the approximate area of a moose survey unit). Sampling regions were centered on the midpoint of moose survey units. Pixels within the sampling region were extracted for analysis. The area of the sampling region was increased by 50% and the pixel extraction was repeated. Processing was halted after six iterations so that the edge of the sampling region would not extend beyond the most distant edge of the adjacent survey units. The maximum sampling region approximated a 3 × 3 grid of moose survey units. Resultant sampling regions were 15, 22.5, 33.75, 50.63, 75.94, and 113.91 km² with sampling region radii of 2.185, 2.676, 3.277, 4.014, 4.916, and 6.021 km, respectively.

Vegetation classes include nonvegetated (ice, rock, or lichen), low shrub (*Betula glandulosa* and *Betula nana*), deciduous and tall shrub (willow, *Salix* spp.; alder, *Alnus tenuifolia*; balsam poplar, *Populus balsamifera*; paper birch, *Betula papyrifera*; and aspen, *Populus tremuloides*), and spruce (*Picea mariana*, *Picea glauca*). We quantified the availability of riparian and wetland habitats by measuring overall length of rivers within each sample unit and the nearest-neighbor distance from sampling units to riparian habitats. We obtained historic fire grids for Alaska, compiled by the Alaska Fire Service, for each year from 1950 to 2000 (Murphy et al. 2000). We merged fire grids for 1952–1961, 1962–1971, 1972–1981, 1982–1991, and 1992–2000 to form 10-

year intervals. The original fire grids contained no data in pixels where fire had not occurred in that particular year or interval. We processed these 10-year grids to replace these null values, which represented unburned areas, with a numeric value (no fire = 0, fire = 1). We derived landscape metrics from the computer program FRAGSTATS (McGarigal and Marks 1995; Table 1).

We produced a correlation matrix of all explanatory variables to investigate whether they were interrelated (collinear). Collinear variables can make interpretation of regression models difficult (Mosteller and Tukey 1977: 280). Whenever variables had a correlation coefficient (r) that exceeded 0.70, we dropped one of the variables, keeping the one that we judged as being more proximate to changes in moose density. We included the remaining explanatory variables in a spatial linear model.

Model selection

Initially, we wanted to account for a trend surface of very coarse-scale patterns in our data. The data set consists of many different management areas in Alaska, and moose density has broad geographical patterns due to extensive changes in climate and geography and different management patterns and predation levels. In addition to the explanatory variables described earlier, we included a fourth-order polynomial on the x - and y -coordinates to spatially model this coarse-scale pattern (Fig. 2a). There are dramatic differences among various management areas, which can be seen in their physical separation from other groups of points (Fig. 2a). Figure 2b shows the residuals after subtracting the fitted trend surface from the raw data; these residuals show that the finer scale pattern within areas remains, but there are no longer dramatic differences among areas. In terms of a geostatistical model, this helps satisfy the assumption of stationarity (e.g., Cressie 1993, p. 52). We tried several orders for the polynomial. Based on visual inspection of the residuals for stationarity and inspection of residual Q - Q plots for assessing normality, we chose the fourth order as the most appropriate model. We computed empirical semivariograms (Cressie 1993, p. 75) on the residuals to examine anisotropy (Cressie 1993, p. 64) and concluded that an isotropic covariance model was sufficient.

Development of a spatial linear model

We used a spatial linear model to analyze the data (Ver Hoef et al. 2001). The spatial linear model can be written as

$$y = \mathbf{X}\beta + \varepsilon$$

where y is a vector for the response variable (log of female moose density), \mathbf{X} is a design matrix containing the explanatory variables, β is a vector of parameters, and ε represents random error. Classical linear models assume that $\text{var}(\varepsilon) = \sigma^2\mathbf{I}$; that is, all errors are independent. We relax this assumption and allow the errors to be spatially autocorrelated, so $\text{var}(\varepsilon) = \Sigma_\theta$, where Σ_θ is the covariance matrix, and we show its dependence on spatial autocorrelation parameters θ . Autocovariance is modeled based on the distances between all pairs of points. We used the exponential model

$$C_\theta(h) = \theta_1 I(h = 0) + \theta_2 \exp(-h/\theta_3)$$

where h is the distance between any two points, $I(a)$ is the indicator function (equal to one if the expression a is true,

Table 1. Description of spatial variables in interior Alaska for each of six sampling regions centered about each moose survey unit center point (2001).

Variable	Description
Geographic feature	
Towndist	Distance of moose survey unit center point to nearest town
Rivdist	Distance moose survey unit center point to nearest river
Rivlen	Total length of rivers within sampling region
Elev	Mean elevation
Drain	Mean drain (actually a categorical variable, wet to dry)
Slope	Mean slope (degrees)
Landcover	
fire52, fire62, fire72, fire82, fire92	No. of burned pixels for each 10-year fire class
VEG1	No. of nonvegetated pixels
VEG2	No. of low shrub pixels
VEG3	No. of deciduous and tall shrub pixels
VEG4	No. of spruce pixels
Terrain	
Xmn	Aspect mean angle, x-coordinate
Ymn	Aspect mean angle, y-coordinate
Rmn	Length of mean aspect vector
Smn	Mean angular deviation
Slsd	Standard deviation of slope
Tvi	Terrain variability index
Landscape metric	
ED	Edge density
AREA_MN	Mean patch size
AREA_CV	Patch size coefficient of variation
SHAPE_MN	Mean shape index
SHAPE_CV	Shape index coefficient of variation
FRAC_MN	Mean fractal dimension
FRAC_CV	Fractal dimension coefficient of variation
ENN_MN	Mean euclidean nearest-neighbor distance
CWED	Contrast-weighted edge density
ECON_MN	Mean edge contrast index
CONTAG	Contagion index
PRD	Patch richness density

Note: We merged fire grids for 1952–1961 (fire52), 1962–1971 (fire62), 1972–1981 (fire72), 1982–1991 (fire82), and 1992–2000 (fire92) to form 10-year intervals. We calculated landscape metrics using FRAGSTATS (McGarigal and Marks 1995) for the vegetation grids and for each of the five fire intervals.

otherwise it is zero), and the vector θ only contains three parameters: the nugget θ_1 , partial sill θ_2 , and range θ_3 . The goal of analysis is to estimate β and θ ; β contains the parameters of our linear model. To estimate β and obtain variances of these estimates, we need to know θ . Because of large sample sizes, our data posed some difficulties, and our solution requires some explanation.

We chose restricted maximum likelihood (REML) to estimate θ . The usual geostatistical methods of estimating variograms, for example, weighted least squares (see Cressie 1993, p. 96), are not appropriate here because we are modeling the errors, which are not observable directly. For these instances, maximum likelihood (ML) and REML are better. Between the likelihood methods, ML is known to be more biased than REML (Mardia and Marshall 1984; Ver Hoef and Cressie 2001). REML creates a likelihood that depends on θ only, by integrating over all possible values of β , and then we only needed to maximize this likelihood. The maximization pro-

cedures, however, are iterative and involve the inverse of Σ_θ for each iteration, a 2628×2628 matrix in our case. In this instance, Stein (1999, p. 172) recommended creating subregions, computing the likelihood for each subregion, multiplying those likelihoods, and then maximizing. This procedure should lead to little loss of information. Stein (1999) also recommended at least 100 observations per subregion. We divided our data into 10 subregions, each of which had >200 observations (Fig. 1).

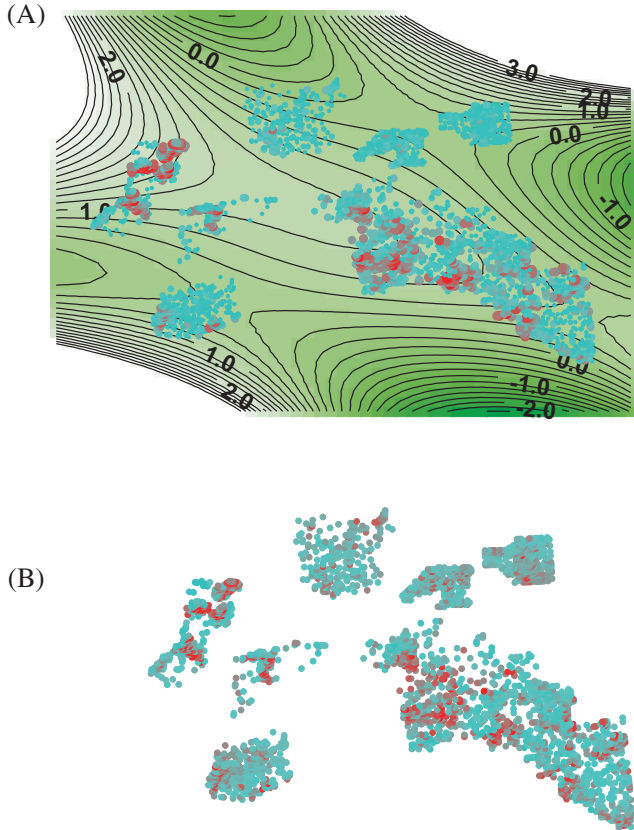
Once θ was estimated ($\hat{\theta}$), we proceeded with generalized least squares,

$$\hat{\beta} = (\mathbf{X}' \Sigma_{\hat{\theta}}^{-1} \mathbf{X})^{-1} \mathbf{X}' \Sigma_{\hat{\theta}}^{-1} \mathbf{y}$$

to estimate the regression parameters, and their estimated variances are the diagonal elements of

$$\text{var}(\hat{\beta}) = (\mathbf{X}' \Sigma_{\hat{\theta}}^{-1} \mathbf{X})^{-1}$$

Fig. 2. (A) The large-scale trend surface fitted to the moose survey data. (B) Residuals from the trend surface. For both figures, the larger red circles indicate higher values, and the smaller blue circles indicate lower values. Survey data were collected for female moose by federal and state management agencies in interior Alaska, USA (1998–2001).

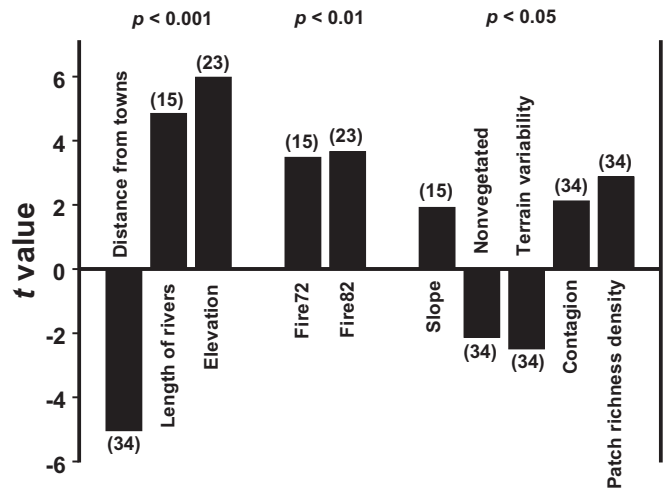


Note that for generalized least squares, we used the full $2628 \times 2628 \Sigma_{\theta}$, which only needs to be inverted once. For evaluating the importance of explanatory variables, we created Student's t values, the estimated regression coefficient divided by its standard error. These t values incorporate spatial autocorrelation in their estimates and standard errors. All parameters of β and θ were fit with PROC MIXED in SAS (SAS Institute Inc. 1999).

Developing a predictive model

We based our stratification on predictions made by area biologists who forecast areas that they expect to have high and low densities of moose based on biological knowledge and surveys conducted in the previous year. The resultant stratification is simple because the entire region of interest is separated into two strata, expected high and low densities. During moose surveys, more intensive sampling is conducted in areas believed to be high density. We developed a predictive model to determine the efficacy of using our spatial linear model to gain greater precision in delineating survey units. We used survey data collected in Game Management Unit (GMU) 20D in and around the town of Delta Junction, Alaska, in 2001. These data were not used as part of the model estimation and were held back as a validation data set. Consider the linear linear model again

Fig. 3. Student's t values of explanatory variables that were significantly related to female moose densities after correcting for large-scale trend. Numbers in parentheses correspond to the scale at which that variable was most significantly related to density of female moose.



$$\begin{pmatrix} y_s \\ y_u \end{pmatrix} = \begin{pmatrix} X_s \\ X_u \end{pmatrix} \beta + \begin{pmatrix} \epsilon_s \\ \epsilon_u \end{pmatrix}$$

where the subscript “s” indicates sampled and the subscript “u” indicates unsampled. All unsampled locations are predicted by the universal kriging equations (Cressie, 1993, p. 151), which can be written as

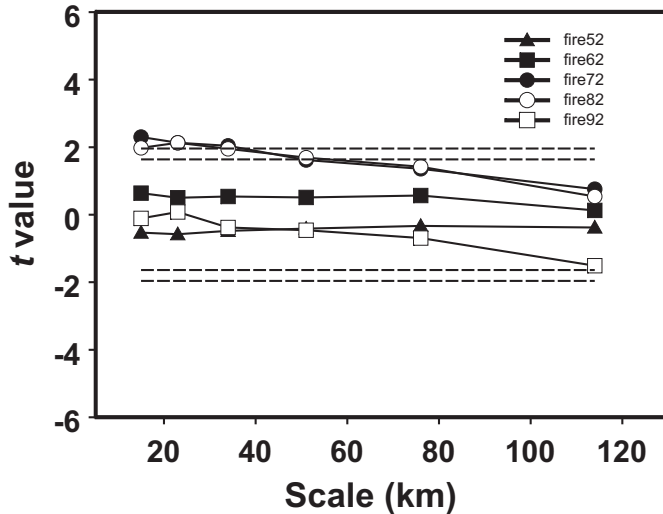
$$\hat{y}_u = X_u \hat{\beta} + C_{\hat{\theta}} \Sigma_{\hat{\theta}} (y_s - X_s \hat{\beta})$$

where $\hat{\theta}$ is the REML estimate of the covariance parameters, $\hat{\beta}$ is the generalized least-squares estimate of the linear model parameters, $\Sigma_{\hat{\theta}}$ is the estimated covariance matrix among the observed data, and $C_{\hat{\theta}}$ is the estimated covariance matrix between the observed and unobserved data. Notice that the universal kriging equations have two parts; a prediction based on the linear model $X_u \hat{\beta}$ (i.e., as in a prediction from a regression model) and an adjustment for local, spatially autocorrelated effects $C_{\hat{\theta}} \Sigma_{\hat{\theta}} (y_s - X_s \hat{\beta})$. All unsampled units were predicted in this way. We then compared predicted values with those that were observed in GMU 20D in 2001. We exponentiated predictions to put them back on the scale of the observed data. We simply present a scatter plot for comparison; further statistics on comparisons are complicated by the correlations in the predictions (beyond autocorrelation) and autocorrelation in the validation data set, so we have not attempted them.

Results

The most significant effects of individual variables (t values, the estimated regression coefficient divided by its standard error) in analyses (Fig. 3) revealed that the densest populations of moose occurred closer to towns ($t = -5.04$), at moderate elevations ($t = 5.98$), and in areas with greater amounts of riparian habitat ($t = 4.85$). Each of these effects was significant at all scales examined in this study (data not shown). The densest populations of moose also occurred in areas where fire occurred between 11 and 30 years ago ($t = 3.66$ for 11–20 years, and $t = 3.48$ for 21–30 years). In addition,

Fig. 4. Student's t values of the relation between explanatory fire-history variables and the residual female moose densities of Fig. 2B.



tion, moose tended to occur in areas that had large ($t = 2.12$), compact ($t = 2.87$) patches of varied habitat and avoided variable terrain ($t = -2.49$) and nonvegetated areas ($t = -2.13$). Significant relationships of these variables with moose density occurred at or below 34 km², which suggests that moose respond to environmental variables within a few kilometres of their location.

An evaluation of t values across all scales indicated that there was no association of moose with habitats that had burned >30 years ago or that burned in the last 10 years (Fig. 4). Moose density was positively associated with habitats that had burned between 11 and 30 years ago across all scales, although the relationship was only significant at 15- and 23-km² scales. For habitats that burned between 31 and 40 years ago, moose density showed a positive but not significant association across all scales.

Predictions made for GMU 20D in Alaska from the final model resulted in a fairly complicated pattern of female moose distribution (Fig. 5), particularly when compared with stratification results derived from the local biologists for the portion of the GMU south of the Tanana River (Fig. 6a). The final model, which also includes survey information from the previous year and information on habitat, terrain, and fire history, provides the ability to predict density and distribution of moose in GMU 20D in a continuous fashion (Fig. 6b). A subsequent survey of all moose in Unit 20D-South was highly correlated with predictions of female moose density by the model (Fig. 7).

Discussion

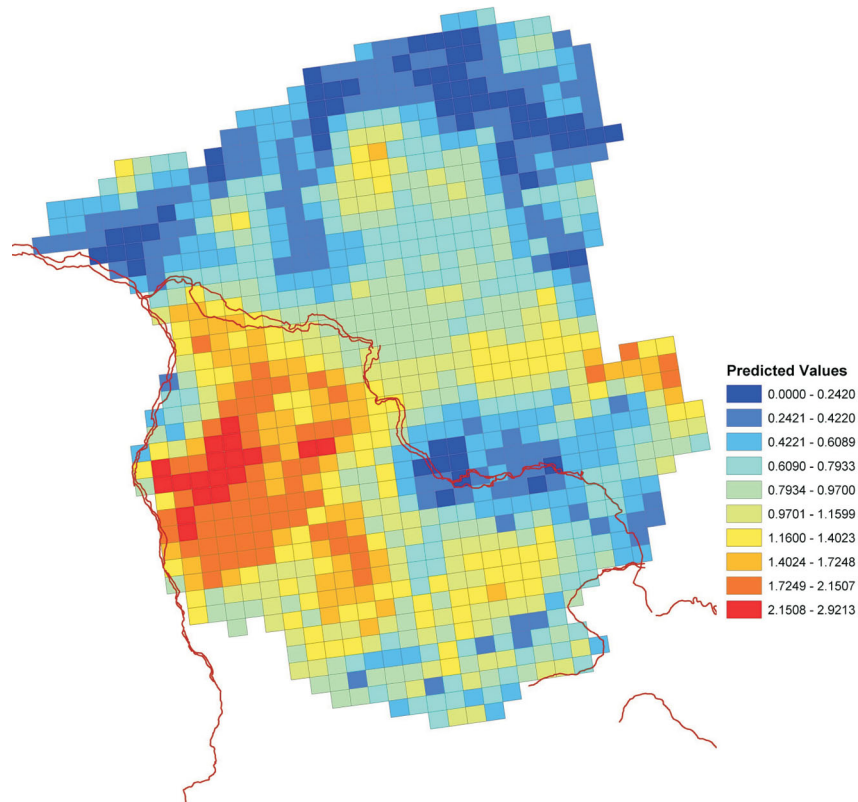
The spatial variability of absolute moose density in Alaska is primarily influenced by local factors that are related to the historical dynamics of individual populations. These factors may include the effects of deep snow years, fire effects on vegetation, range condition, interactions between predator populations (including humans) and moose population dynamics, and the history of game management and human

land use in a particular area (Gasaway et al. 1983, 1992). By incorporating a large-scale trend of population density of female moose, our analysis evaluated landscape-level factors influencing moose density across the spatial domain of analysis while holding between-area differences in moose density constant. The three most significant variables in the analysis indicated that moose tended to occur at higher densities in areas with extensive river margin, in areas with moderate elevation, and in areas closer to towns. It is important to note that these relationships, and in particular the distance to towns, were significant at all scales examined in this study. The connection with the amount of river margin is consistent with the analysis of Jandt (1992) in western interior Alaska and is readily understandable because river margins are disturbed habitats that promote the growth of willows, an important food for moose (Bowyer et al. 2003). Moose generally move from higher elevations to the lowlands between autumn and winter. Thus, the association of higher female moose density with higher elevations was likely the result of surveys being conducted in late autumn (generally November). Moose may have been transitioning between rutting and winter ranges during this period. Moose tend to spend winter months in low-elevation riparian habitats to take advantage of lower snow accumulation (Doerr 1983; Collins and Helm 1997), high-quality forage, and high diversity of successional conditions (Miquelle et al. 1992; Collins and Helm 1997). Additionally, upland habitats likely are more affected by fire disturbance than are riparian habitats, since wetter environments are less likely to burn (Thompson et al. 2003, but see Harden et al. 2003). Consequently, measuring density of moose over the period in which they are using habitat that may be highly impacted by the fire regime is essential to understanding the heterogeneous pattern of burns on the landscape.

The association of higher densities of moose near towns was also reported for moose in northern Alberta (Schneider and Wasel 2000) and may be related to two factors. First, because vegetation near towns is generally disturbed, moose may occur close to town to take advantage of high-quality foods (Schneider and Wasel 2000). An alternative hypothesis to explain the increased density of moose near towns is the reduced density of natural predators such as wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) near towns. Wolves and bears are intolerant of human habitation (Weaver et al. 1996; Sidorovich et al. 2003; Theuerkauf et al. 2003) and are reduced or eliminated near towns via hunting and trapping. We cannot identify which of these factors may be more important; further research is required to evaluate this issue.

Our analysis revealed that moose use areas that burned between 11 and 30 years ago, but that there is still a positive association of moose with areas that burned between 31 and 40 years ago. This pattern is consistent with analyses for the Kenai Peninsula in Alaska, including the conceptual model of Schwartz and Franzmann (1989) and field studies by Loranger et al. (1991) and Weixelman et al. (1998). Fire is the major disturbance of boreal forests in interior Alaska. For example, an average of 300 000 ha/year burned annually in Alaska between 1960 and 2000 (Kasischke et al. 2006), which represents between 0.5% and 1% of the boreal forest in interior Alaska (McGuire et al. 2002). More than 1.5×10^6 ha has burned in a single year (Kasischke et al. 2006).

Fig. 5. Predictions of the log of female moose density for Game Management Unit 20D near Delta Junction, Alaska, USA, based on application of the spatially explicit model developed in this study. Unit 20D-South is below the Tanana River, which bisects the management unit.



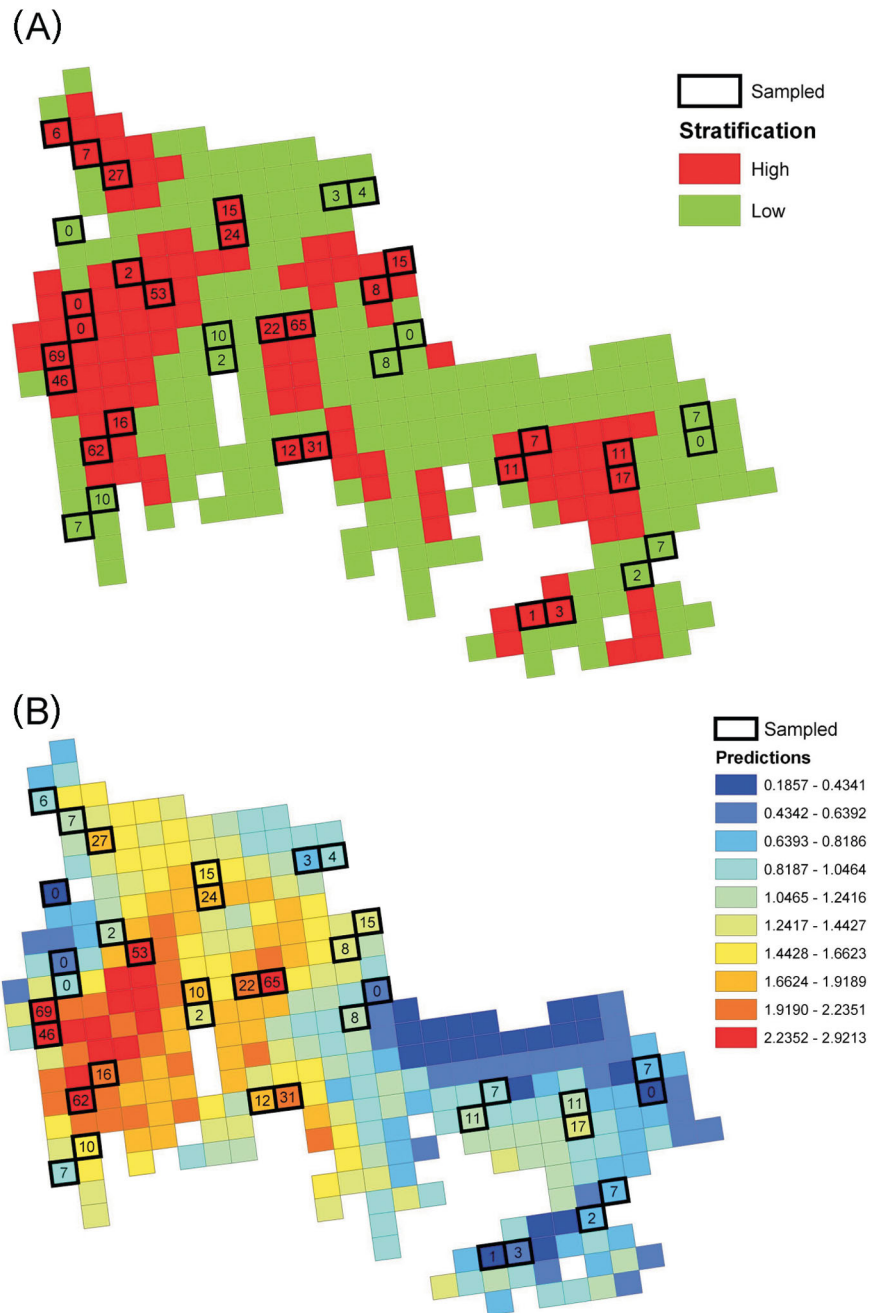
The successional pattern of vegetation in Alaska often results in substantial growth of deciduous shrubs after fires, which are preferred in the diet of moose (Van Ballenberghe et al. 1989; Weixelman et al. 1998). For the first few years after a fire, however, there can be variability in plant regeneration both in terms of species presence and timing of recolonization. Willow has an advantage establishing itself just after a fire because it can both regenerate clonally and disperse by seed. As succession proceeds, the shrub layer will eventually develop so that it emerges above the snow in winter (Weixelman et al. 1998). As stands age, deciduous shrubs are replaced by spruce in boreal landscapes. These patterns of succession explain the positive association of moose for areas that have burned between 11 and 30 years ago and the neutral association for the areas that have burned less than 10 years ago and more than 30 years ago. Consequently, moose density increases hypothetically within 5–10 years after a fire on the Kenai Peninsula (Schwartz and Franzmann 1989) and reaches its highest point sometime in the 13- to 26-year time span (Loranger et al. 1991). In agreement with this hypothetical model, our analyses indicate that moose in interior Alaska occur at higher densities in areas 11–30 years after fire.

Although moose densities are positively associated with the amount of river margin and with elevation, other terrain variables also appear to play a role in determining moose density. Our analyses revealed that moose avoid nonvegetated areas, and thus their association with higher elevations appears to be truncated at elevations at which vegetation gives

way to rock and ice, an outcome also noted by Bowyer et al. (1999). We did not find associations with vegetation type, which may be the result of not being able to distinguish between palatable deciduous shrubs (e.g., willow) from unpalatable deciduous shrubs (e.g., dwarf birch) and trees (e.g., paper birch) in the vegetation coverage we used in our analyses. Alternatively, moose may be responding to forage at a finer spatial scale than we measured in this study. Bowyer et al. (1999) demonstrated that moose in Denali National Park, Alaska, selected birth sites based on microsite characteristics of the surrounding habitat. Moose likely are relating to their environment on multiple scales, as do other large herbivores including woodland caribou (*Rangifer tarandus*, Johnson et al. 2001; 2002) and elk (*Cervus canadensis*, Boyce et al. 2003). The positive association of density of female moose with slope and negative association with terrain variability indicate that moose prefer moderate slopes in settings with unchanging topographic relief.

The positive association of density of female moose with patch richness density reveals that female moose prefer areas of varied habitat, indicating their need for a diverse habitat including food and availability of concealment. Forage selection theory indicates that large generalist herbivores such as moose will select a mixed and balanced diet to maximize nutrient intake, and indeed they do (Belovsky 1981; Irwin 1985; Hjeljord et al. 1990; Saether and Andersen 1990; Shipley et al. 1998; Edenius et al. 2000). A varied habitat also provides areas of dense cover that may be important for concealment from predators (Molvar and Bowyer 1994). The

Fig. 6. (A) A two-level stratification of moose densities assigned by an area biologist of the Alaska Department of Fish and Game for Game Management Unit 20D-South (the area south of the Tanana River in Fig. 5) near Delta Junction, Alaska, USA, and (B) the predictions of the log of female moose density by the spatially explicit model developed in this study (see Fig. 5). The survey counts of total moose are shown by those grid cells containing numbers with heavy borders.

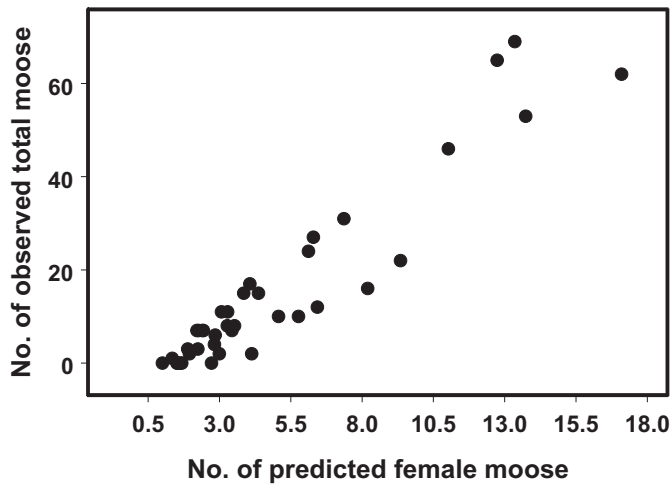


positive association of density of female moose with the contagion index indicates that female moose prefer large compact patches of vegetation rather than interspersed patches; yet this result may be erroneous. Given that there is a positive association of density of female moose with patch richness density, which is inversely related to contagion, we would expect a negative association between contagion and density of female moose. Contagion is often overestimated when it is calculated using data with variable and (or) large pixel sizes (Greenberg et al. 2002). Unfortunately, the data set available for use in delimiting vegetation types for inter-

rior Alaska is characterized by large pixels of variable sizes. Future research efforts should focus on ascertaining relations between density of moose and landscape metrics in local areas that are represented by high-quality remote sensing images.

Significant relationships of most variables with moose density occurred at or below the 34-km² scale, which indicates that moose respond to environmental variables within a few kilometres of their location. The resolution of our analyses was limited to the 15-km² scale because estimates of female moose density were developed at this resolution. Some of the nonsignificant or less significant variables we analyzed

Fig. 7. A comparison of total moose counted during an aerial survey near Delta Junction, Alaska, USA, in 2001, with the number of predicted female moose from the application of the spatially explicit model developed in this study.



in this study may become more significant if the analyses can be conducted at a finer resolution than 15 km².

We applied the spatial model developed in this study to predict the spatial variability in the density of female moose of a particular game management unit (Unit 20D) near Delta Junction, Alaska, in late autumn. The validation of the model indicates that this analysis provides more accurate information across the landscape because of its rather gradual transition along a density gradient in comparison with the two strata (i.e., low and high density) that have traditionally been used by area biologists to design surveys. Therefore, the results of the model provide a basis for fine-tuning survey designs to better estimate moose populations in an area. The model developed in this study represents an important tool that can be used to improve the monitoring and the management of moose populations in interior Alaska.

Conclusion

The development of an understanding of how habitat heterogeneity influences the distribution and population dynamics of large herbivores has been a challenge in ecology because landscapes are inherently dynamic and herbivores perceive their environment at multiple scales (Kie et al. 2002, 2003). Yet this understanding is important for effective monitoring and management of populations of large herbivores, which play important roles in the dynamics of ecosystems and are often important for cultural and economic reasons. The analyses in this study revealed that a number of landscape variables influence moose density at relatively small scales (≤ 34 km²) and that these variables tend to become less important at larger scales. Relationships between moose density and habitat heterogeneity may occur at spatial scales finer than that examined in this study, but the resolution of analyses was limited because the sampling of moose density was conducted at a resolution of approximately 15 km². The most important variables related to moose density at the scales evaluated in this study are elevation and proximity to rivers and towns. Other landscape variables related to density of moose at small scales included avoidance of nonvegetated

areas and variable terrain and the affinity of moose for areas where fire has occurred within the previous 11–30 years. Furthermore, moose tended to occur in areas of large compact patches of varied habitat. Each of these variables can be related to what is known about the various habitat requirements of moose in interior Alaska. Besides providing insights into the relative importance of the various components of habitat heterogeneity on the density of moose, the analyses also provided information to develop a spatial model of moose population density that represents an important tool for more effective monitoring and management of moose in interior Alaska.

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