Development and application of a spatially explicit moose population model

Daniel W. McKenney, Robert S. Rempel, Lisa A. Venier, Yonghe Wang, and Alan R. Bisset

Abstract: We developed spatially explicit models of moose (*Alces alces*) population density for the province of Ontario using the geostatistical technique kriging. The models were based on moose surveys divided into four time periods from 1975 to 1995. Density change was calculated for the 1975–1979, 1980–1984, 1985–1989, and 1990–1995 time periods to visualize regional trends in population change. Between 1975 and 1995, moose density increased in the northwest and southeast parts of the province and decreased in some northern pockets. A marked increase in density occurred in the late 1980s, when both the selective moose harvest system and moose habitat guidelines were introduced in Ontario. Although a general increase in survey effort occurred in about 1986, no effect of survey effort was detected on moose population change between the first and last time periods ($P = 0.215$). To evaluate the possible effect of reducing number of survey plots on density estimates, we recreated density maps by using 25, 50, and 75% of the original data and compared the full-data maps with the reduced-data maps. The regression slopes and r^2 for reduced-data versus full-data maps approached 1.0 as sample rate increased from 25 to 75% ($B = 0.88$, 0.86, and 0.96; $r^2 = 0.82$, 0.88, and 0.95). A κ analysis also suggests an acceptable performance of the 75% data map ($\kappa = 0.716$).

Résumé : Nous avons conçu des modèles spatiaux de densité des populations d'orignaux (*Alces alces*) de la province d'Ontario au moyen d'une technique géostatistique, le krigage. Les modèles sont basés sur des recensements d'orignaux divisés en quatre périodes de 1975 à 1995. Les changements de densité ont été calculés pour les périodes 1975–1979, 1980–1984, 1985–1989 et 1990–1995 afin de permettre la visualisation des tendances régionales des changements de densité. Entre 1975 et 1979, la densité des orignaux a augmenté dans les sections nord-ouest et sud-est de la province et a diminué dans certaines zones isolées du nord. Une augmentation marquée de la densité a été enregistrée à la fin des années 80, alors qu'un système de chasse sélective des orignaux et des directives sur l'aménagement de leur habitat ont été introduits en Ontario. Bien qu'il y ait eu une augmentation générale de l'effort de recensement vers 1986, cette manoeuvre n'a pas eu d'effet sur l'évolution de la population d'orignaux entre la première et la dernière période ($P = 0{,}215$). Pour évaluer les effets possibles d'une réduction du nombre de zones recensées sur l'estimation des densités, nous avons fait des cartes de densité utilisant 25, 50 et 75% des données originales et comparé les cartes basées sur les données intégrales et les cartes basées sur les données partielles. Les pentes des régressions et le r^2 des données partielles, comparativement aux données intégrales, s'approchaient de 1,0 à mesure que le taux d'échantillonnage augmentait entre 25 et 75% ($B = 0{,}88$, 0,86 et 0,96; $r^2 = 0{,}82$, 0,88 et 0,95). Les résultats d'une analyse κ soulignent aussi la performance acceptable de la carte basée sur 75% des données intégrales ($\kappa = 0{,}716$).

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Introduction

Wildlife management often requires a capacity to spatially extend field observations beyond the locations where surveys have been conducted. For example, Ontario is a large Canadian province (about 1×10^6 km^2) and wildlife management is conducted over vast areas that cannot possibly be thoroughly surveyed every year. Techniques for spatially extending survey data are essential in this context. Recent advances in geostatistical methods have provided methods for spatial interpolation of site data over large areas (Isaaks and Srvivastava 1989). Kriging, a method of spatial interpolation, has been used to create maps of the distribution and abundance of many taxa, including decapod crustaceans (Maynou et al. 1996), weeds (Donald 1994; Heisel et al. 1996), herring (Maravelias and Haralabous 1995), gypsy moth (Gribko et al. 1995; Weseloh 1996), and songbirds (Villard and Maurer 1996). Kriging has also been used to interpolate climate data from point samples at weather stations (Hammond and Yarie 1996; Holdaway 1996) and in soil sci-

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D.W. McKenney, L.A. Venier, and Y. Wang. Natural Resources Canada, Canadian Forest Service, Sault Ste. Marie, Great Lakes Forestry Centre, P.O. Box 490, 1219 Queen Street East, Sault Ste. Marie, ON P6A 5M7, Canada.
R.S. Rempel.[1] Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Lakehead University Campus, 955 Oliver Road, Thunder Bay, ON P7B 5E1, Canada.
A.R. Bisset. Ontario Ministry of Natural Resources, Box 5160, Kenora, ON P9N 3X8, Canada.

[1] Author to whom all correspondence should be addressed (e-mail: rempelr@gov.on.ca).

ence to map soil characteristics (Odeh et al. 1994; Halvorson et al. 1995; Boyer et al. 1996).

In this study, we developed several spatially explicit models of moose (*Alces alces*) population density for the province of Ontario using kriging techniques. The Ontario Ministry of Natural Resources has been managing moose since 1955 (Timmermann and Whitlaw 1992). Data from aerial surveys for moose have been compiled in a computer data base for large areas of central and northern Ontario dating from 1975 (Bisset and Rempel 1991). Our models estimate and visualize densities and abundance of moose in these areas during four time periods from 1975 through 1995. Creating maps of the population estimates over time enabled us to provide an instantaneous view of population change (see also Villard and Maurer 1996). Population change would not be expected to be uniform in size or direction over the entire province; hence, a spatially explicit picture of trends provides insights beyond what could be provided by a single numerical estimate. These new data may in fact be useful for landscape-level assessments of the causes of population change. Generally, kriging should provide more robust density estimates than averages of sites surveyed within a wildlife management unit (WMU) because it includes information from neighbouring areas.

Ontario is divided into WMUs of various sizes that serve as the basis for estimating population sizes and administering hunting tags in the province. To support management applications, we used our 1990–1995 model to rank the relative densities of moose across all WMUs. This provides an indicator of the relative importance of each WMU against the most “moose-dense” WMU. Aerial surveys are costly and the number of surveys is being reduced because of fiscal constraints in the province. We also rebuilt the 1990–1995 spatial model with subsets of the survey data to investigate the implications of reduced sampling on population estimates.

Materials and methods

Moose surveys

Aerial moose surveys were conducted from 1975 to 1995 following set Ontario standards (Bisset 1991). Light, fixed-wing aircraft were used for surveys from 1975 to 1985, but many districts switched to helicopters from 1986 onward. A single survey plot covered an area of 25 km^2, and survey areas are based on a regular UTM grid (Fig. 1). For each plot, we determined the geographic centre and recorded this as a UTM coordinate. We divided the data into four periods (1975–1979, 1980–1984, 1985–1989, 1990–1995) rather than annually to ensure that there were sufficient surveys to adequately cover the study area (see Fig. 1 for locations and survey numbers). The number of surveys in each of the four time periods is similar.

Each WMU (Fig. 2) was surveyed approximately every 3–5 years, with the surveys conducted during winter months at locations randomly selected each year (Bisset and McLaren 1995). The total number of cows, calves, and bulls viewed by the observer was recorded. Total time spent on each survey plot was also recorded. For each 5-year time block, we calculated the average number of moose observed per year per 25 km^2. Track aggregates are sometimes used to estimate the number of missed moose. However, the application of this technique varies among regions, years, and individual biologists; hence, we chose not to adjust density values by estimates of the number of moose missed. Thus, our estimates may underestimate absolute total density. However, the relative density estimates and trends should be comparable among regions and years.

Spatial model

Spatial modelling of the survey data was performed using the ordinary kriging technique. The essence of the kriging is to estimate the unknown value at a point using a weighted linear combination of the samples available in the neighbourhood of the point (Isaaks and Srivastava 1989; Olea 1991). In our application the spatial correlation in abundance over an area is used to predict (estimate) the abundance over nonsampled areas. Let u be the grid cell representing the geographic location of the point to be estimated and Z the value to be estimated, i.e., the number of moose per 25 km^2. If u_i, $i = 1, 2, ..., N$, are the geolocations of the N sample plots, then $Z(u_i)$, $i = 1, 2, ..., N$, are the observed moose counts at the points. Ordinary kriging was used to calculate the kriging weight $v_i(u)$, $i = 1, 2, ..., N$, based on the values and distances between these locations. The estimated moose count at location u is a summation of $w_i v_i(u)$, where w_i are the weights determined by the sample data. The reason we chose the ordinary kriging technique is because we believe that moose populations in the region have an overall stationary distribution that makes ordinary kriging appropriate.

We assumed that azimuth direction is unlikely to play any role in the distribution of moose; hence, we chose an omnidirectional semivariogram to describe the variance in the original data as a function of geographic distance. Several functions are available (Deutsch and Journel 1992). After several tests, we found the following exponential semivariance function best described the data:

$$[1] \qquad \gamma(h) = c\left[1 - \exp\left(-\frac{h}{a}\right)\right]$$

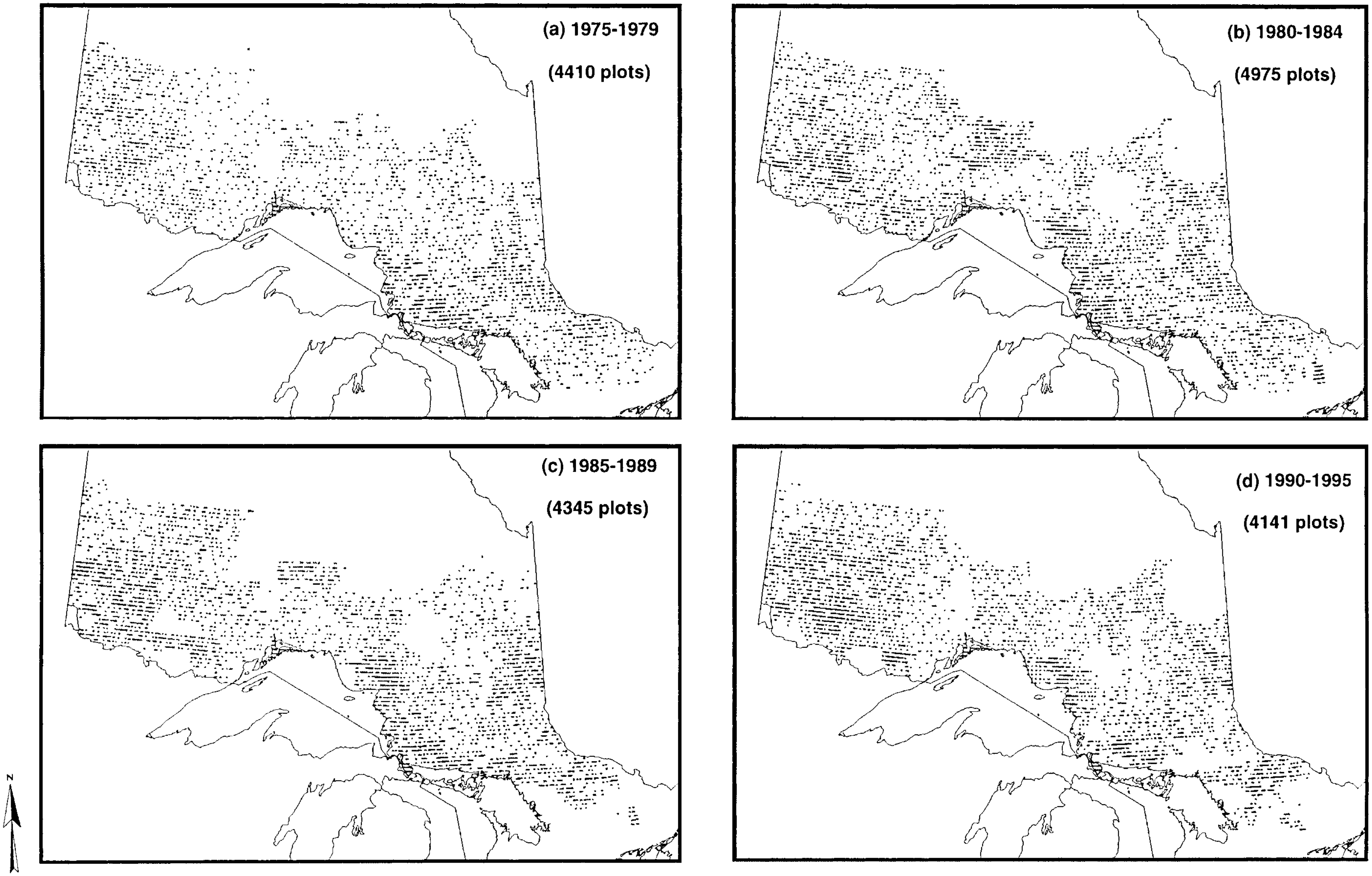
where c and a are two parameters to be estimated from the sample and h is the distance between any two location points; c is referred to as the sill, which represents the variance of the data in the region, and a is called the range, the distance at which the data are no longer autocorrelated (MathSoft Inc. 1996).

Generally, the separation vector h is specified with some distance tolerance (Deutsch and Journel 1992). Equation 1 was calculated for $h = 0$ to $h = 50$ km with the assumption that when the distance between any two locations is greater than 50 km, the autocorrelation between the two points is nonexistent. Nonlinear regression (SAS Institute Inc. 1989, 1996) was then used to fit eq. 1 and obtain estimates of c and a. Once the semivariogram is estimated, kriging can take place using the algorithms developed by Deutsch and Journel (1992). The search radius was 30 km, which implies that only survey points that have a distance ≤30 km to the survey location are considered to have an influence. The search distance was based on the average home range (26–31 km^2) for North American moose (Crête 1989) and the results of the semivariogram analysis noted above. The models were resolved to a regular grid of approximately 1×1 km across north-central Ontario for visualization purposes and subsequent further analysis. They provide a spatial prediction of moose density per square kilometre.

WMU estimates from the spatial model

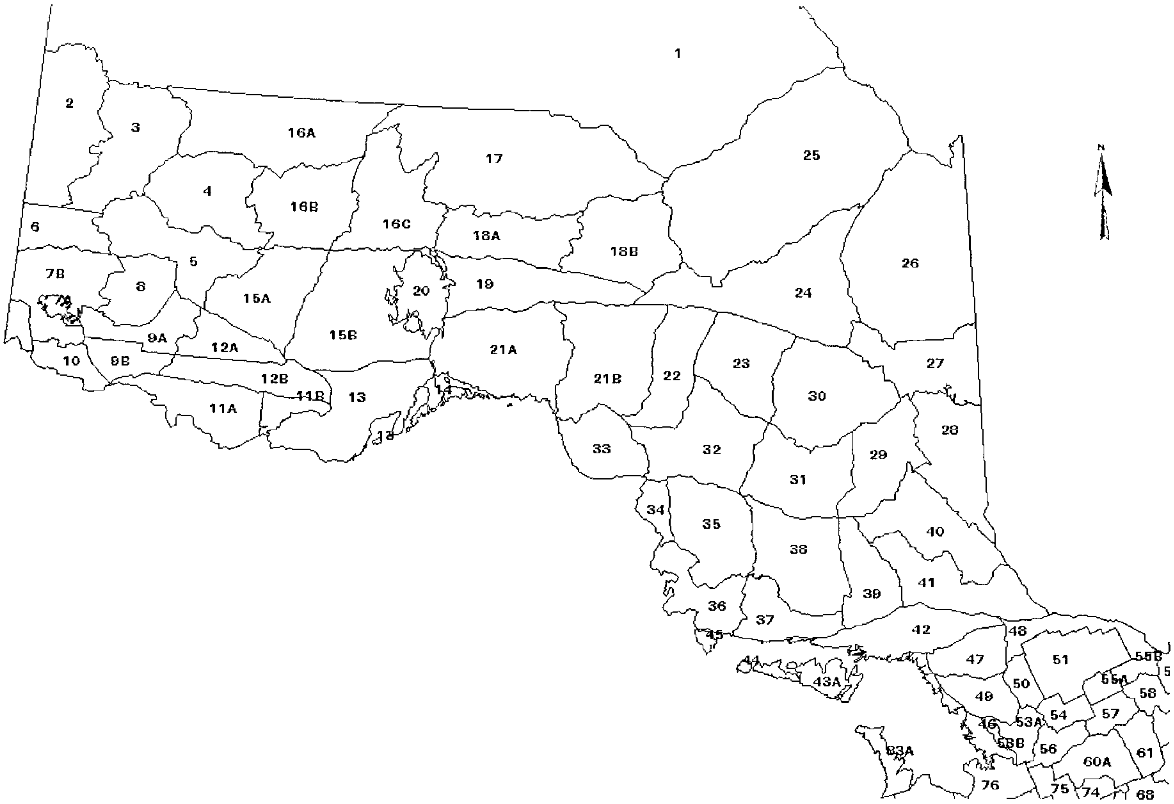
We calculated a weighted average density of the grid cells within each WMU and then estimated the abundance for each WMU by multiplying the average density by the area. As an example application of the density map, we ranked the WMUs in order of average density. We divided the density of the highest WMU by the density at each WMU (following Davis et al. 1994). This indicator identifies the factor by which the density of each WMU would have to increase to equal the most dense WMU.

Fig. 1. Ontario survey locations for four time periods. Each point is located in the centre of 2.5 × 10 km standard moose survey plots.



Projection : Lambert Conformal Conic

Fig. 2. Wildlife management units index map for Ontario within the moose survey area. Algonquin Park is WMU 51.



Density models with fewer data

To investigate possible changes in density estimates due to sample size reductions, we subsampled 75, 50, and 25% of the original data in the 1990–1995 period and repeated the kriging procedure and density estimates. The subsamples were created by removing one, two, or three of every four survey points. Moose survey points were ordered on their geographic location. Linear regression analysis, with regression through the origin, was used to evaluate the influence of reduced sampling rate on moose density estimates over a continuous surface. Corresponding pixel values from moose density maps based on 25, 50, and 75% of available moose survey plots were regressed against pixel values from the moose density map derived from the full complement of moose survey plots. A slope of 1.0 and an r^2 value of 1.0 would indicate perfect correspondence between two maps. Given a regression slope significantly different from 0, slopes >1.0 indicate that the reduced-data map underestimates moose density relative to the full-data map and vice versa for slopes <1.0.

A categorical analysis (κ statistic) was also conducted to measure the agreement between the original map of density and the three maps generated from the subsampled data (Congalton and Mead 1983; Congalton et al. 1983; Congalton 1991). The κ statistic is calculated from a classification table where the rows represent the classes of one map and the columns represent the classes of the second map. The cells of the table contain the proportion of the total number of grid squares that fall into each class combination. The sum of the main diagonal of the table (p_0) is a measure of the agreement between the two maps. The sum of the product of the marginal totals (p_e) represents the chance agreement (Naesset 1996). The κ index can be written as

$$[2] \qquad \kappa = \frac{p_0 - p_e}{1 - p_e}$$

If the agreement is perfect ($p_0 = 1$), then the index is equal to 1; if the observed agreement is low, the index approaches zero. It is also possible to compare the change in agreement between the different levels of sample reduction by comparing error matrices. For reference, we call this the κ comparison (KC):

$$[3] \qquad \mathrm{KC} = \frac{|\kappa_1 - \kappa_2|}{\sqrt{\mathrm{Var}(\kappa_1) - \mathrm{Var}(\kappa_2)}}$$

To derive κ, the density estimates for grid squares must be classified. The classification is somewhat arbitrary and, in general, we found that κ decreases as number of classes increases. Ultimately, we chose to examine a six-level classification density map with intervals of 0.4 moose/km^2. The maximum number of moose ever observed in the 25-km^2 plots was 56 (2.24/km^2); hence, we used 2.4 moose/km^2 as the upper bound for the κ categories.

We also examined the change in density estimates in the WMUs due to reduction in sample size, since management decisions are often made at this scale. The average estimated density for each WMU was calculated using the model based on the original data (100%) and for each subsample of data (75, 50, and 25%). We used analysis of variance, with Student–Neuman–Keuls a posteriori comparisons (Zar 1984) to test for differences of mean density among data reduction models. We calculated the variance in density due to sample reduction for each WMU as

$$[4] \qquad \sum_i (D_{\mathrm{fd}_i} - D_{\mathrm{rd}_i})^2 / n$$

where i = 1–53 WMUs, D_{fd_i} is the WMU density of the full-data model, D_{fd_i} is the WMU density of the reduced-data model, and n is the total number of WMUs. WMUs that were surveyed less often than annually were excluded from this analysis.

Change over time

To visualize spatially the change in population estimates over time, we compared the three time periods (1975–1979, 1980–1984, and 1985–1989) with the most recent time period (1990–1995). We kriged the full data from each time period separately to create a

Table 1. Nonlinear, least squares analysis of semivariogram parameters.

Map period	Parameter	Estimate	Asymptotic SE	Asymptotic 95% confidence limit	
				Lower	Upper
1975–1979	c	13.32	0.246	12.83	13.82
	a	2.57	0.414	1.74	3.40
1980–1984	c	20.77	0.267	20.24	21.31
	a	3.67	0.359	2.95	4.40
1985–1989	c	30.91	0.515	29.88	31.95
	a	4.47	0.494	3.48	5.46
1990–1995	c	45.16	0.611	43.93	46.38
	a	2.70	0.341	2.01	3.39

spatial model of historical population density. The kriging results were grouped into eight classes representing 1, 2, 3, and 4 SDs above and below the mean. A density-change surface was created by calculating the difference of $\log_e$ density for the 1990–1995 and 1975–1979 time periods. The $\log_e$ difference represents the instantaneous rate of population change between the two time periods:

$$[5] \qquad \frac{dN}{dt} = \log_e (N_{t=1}/N_{t=0})$$

where $N_{t=1}$ and $N_{t=0}$ are population densities at times 1 and 0, respectively (Krebs 1984). This map was then smoothed (using a 25×25 mean filter) to identify broad, regional-scale trends in density change. For map presentation, instantaneous rates were back-transformed to finite rates by taking the antilogarithm.

Effects of differential survey effort

Survey effort was not constant over the study period, so we evaluated the effect of differential survey effort on the moose density estimates. We conducted regression analysis to determine the relationship between average time on plot and the instantaneous rate of population increase across 22 WMUs for which we had sufficient survey records of time on plot.

Results

Spatial moose model (1990–1995)

The result of the kriging exercise is a spatial model of moose density within the moose range of Ontario (Fig. 3). An exponential solution (eq. 1) was used to estimate the regional point variance (c) and autocorrelation range (a); the nonlinear least squares analysis, including 95% confidence limits, shows a good fit for both parameters (Table 1).

The average density of moose for 1990–1995 is 0.209 moose/km^2 (Fig. 3*d*), but there is considerable spatial variation, with density ranging from 0.05 to 0.79 moose/km^2. The highest density areas fall in the Algonquin Park area (southernmost region of the study area) and northwestern parts of the province. Lower density areas are scattered throughout the province, and there are some areas with insufficient data to support a spatial prediction using these methods. The 1990–1995 density estimate falls midway between the 1990 estimate of 0.201 moose/km^2 (Whitlaw et al. 1993) and the 1995–1996 estimate of 0.22 moose/km^2 (Bisset et al. 1997). The total population estimate for the province based on this method is 96 390. This compares with a 1990 estimate of 92 883 (Whitlaw et al. 1993). This 4% difference in population estimates is small, and at the provincial scale, it would be expected that both the traditional method of calculating population levels directly from WMU surveys and this kriging approach would yield similar results. The kriging method, however, better captures spatial variability within any given WMU (see Fig. 3).

Densities were also calculated at the WMU level (Table 2). These correspond well to trends in density estimated through traditional methods at the WMU level (Whitlaw et al. 1993). We also ranked the WMUs in terms of density relative to the WMU with the highest density. This provides a relativity index to compare moose densities across WMUs. For example, WMU 7B has the highest density (0.79). WMU 2 has a relative ranking of 3.42, which indicates that the density of this WMU would have to increase by 3.42 times to be the same as that of WMU 7B. Note that ranking WMUs by population estimates (column 5 in Table 2) would change the relative rankings because area is included when estimating population totals for a given WMU.

Change in density estimates due to sample size reduction

Average density and overall population estimates are similar for the model based on all of the data and those based on 75% (0.205 moose/km^2), 50% (0.224 moose/km^2), and 25% of the original data (0.232 moose/km^2). To further examine the effect of sample rate, we computed the slope and r^2 for comparisons of the full-data model versus reduced-data models. Complete agreement would result in both slope and r^2 approaching 1.0, inferring higher accuracy and precision, respectively. As sample rate increased, we found little difference between the 25 and 50% sample rates (B = 0.88 and 0.86, r^2 = 0.82 and 0.88), whereas a marked improvement occurred at the 75% sample rate (B = 0.96, r^2 = 0.95). Hence, maps generated using the 75% sample rate overestimated density (relative to the full-data model) by only 4%.

We felt it informative to evaluate the effects of reduced sample density on the creation of categorical maps. We computed error matrices for each subset of a six-class density map (Table 3). The model based on 75% of the data is closest in classification to the 100% data model (κ = 0.716). This agrees with the regression analysis. The error matrices of the 25 and 50% data models have significantly less agreement (KC = 35.32, $P < 0.05$). The 50% model versus the 75% model has a KC of 69.62 ($P < 0.05$).

We also evaluated the effect of subsampling on density estimates for WMUs. Among the four models based on 100 to 25% data, the average density estimates of 53 WMUs

Fig. 3. Spatial model of moose density in Ontario for four time periods. Resolution (cell size) is 1 km^2. The underlying data are continuous, but for presentation, densities were grouped into six classes based on SDs for the 1990–1995 time period, and the same classes were applied to all four maps. Blue colours indicate where density is below the provincial average (0.209 moose/km^2) and yellow or red colours indicate where density is above the provincial average.

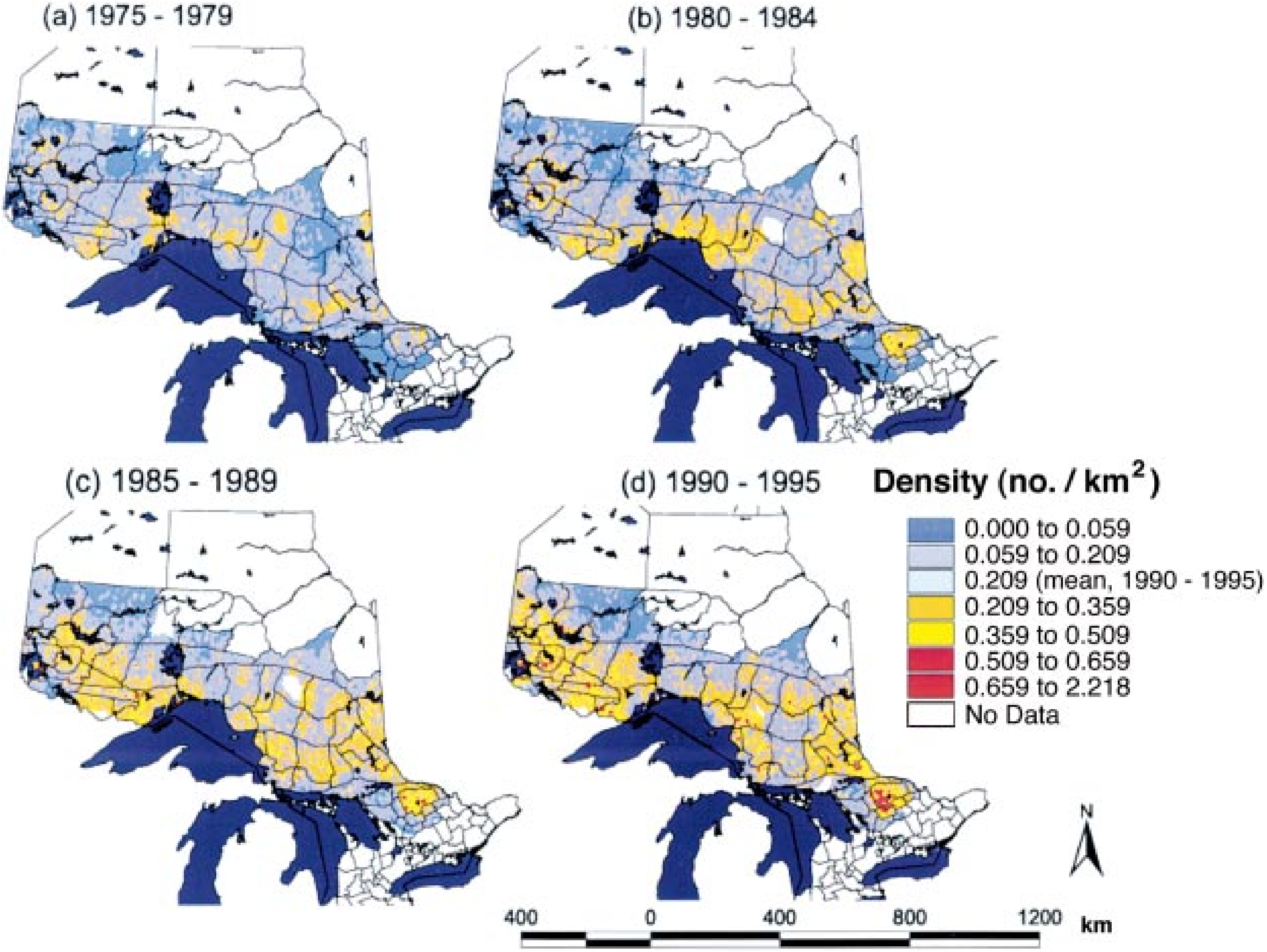
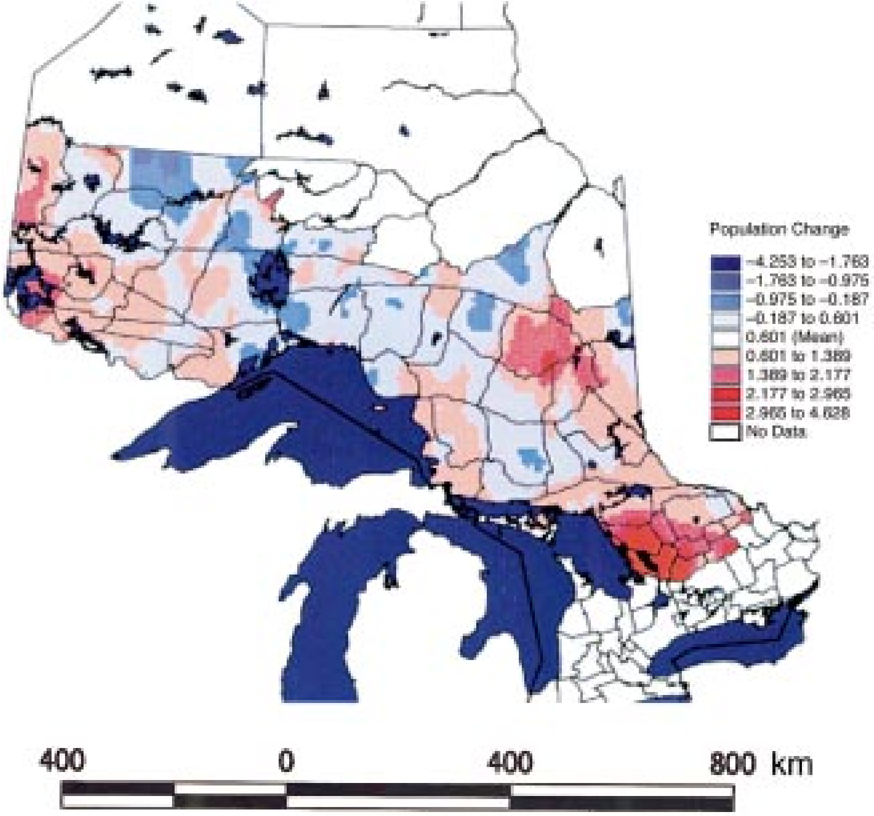


Fig. 4. Rate of change in moose density in Ontario between the 1975–1979 and 1990–1995 time periods. Density change was grouped into eight classes based on 4 SDs above and below the mean finite range of change. Red colours indicate where density change is above the provincial average and blue colours indicate where density change is below the provincial average (e.g., the third red symbol indicates where population has increased 2.177–2.965 times since 1975–1979, and the third blue symbol indicates where it has decreased –0.975 to –0.187 times).



(where moose are surveyed annually) do not differ statistically ($P = 0.9689$) and range from 0.2380 to 0.2499 moose/km^2 (Table 4). At the 75% sample rate, the means differ by only 3.4%. Standard errors of the mean also differ little. This suggests that subsampling had little effect on either accuracy or precision of estimating a provincial-level moose density at this level of aggregation over these time periods. At the individual WMU level, however, the effect of reducing data was much stronger. The average variance of the reduced-data model from the full-data model was three times higher for the 25 and 50% data models than for the 75% data model (Table 5). For all three models, variance for most WMUs was less than about 0.04.

Change over time

Overall, the average moose density is estimated as 0.116, 0.145, 0.179, and 0.209 moose/km^2 for the periods 1975–1980, 1980–1985, 1985–1990, and 1990–1995, respectively. The results show an overall increase of moose during this period, but the change in population abundance is clearly not uniform (Fig. 4). At the regional scale, relative moose density has increased in parts of the northwest, northeast, and southeast (Algonquin), with density increasing by >1 SD than the average rate of change. In north-central Ontario, density has remained relatively unchanged, but with pockets of decline towards the northern limits, where populations in some areas have decreased by more than 1 SD from the average rate of change.

Moose survey effort increased in the province in about 1986 as some districts moved to helicopter surveys from fixed-wing surveys (Bisset and Rempel 1991). The relationship was insignificant between average time spent on plot during surveys and the instantaneous rate of population increase ($P = 0.215$, $r^2 = 0.072$) among 22 of the WMUs, suggesting no effect of differential survey effort on moose density estimates between the first and last time periods. Although larger samples may ultimately demonstrate some effect of increased survey efforts, we believe that the large changes in moose density among the first and last time periods, as seen in Fig. 4, can be only marginally accounted for by differential survey effort.

Discussion

Our approach to calculating density and density change is similar to the methods used by Villard and Maurer (1996) in their study of declines in migratory songbirds. Clear, spatial patterns and temporal trends in moose density emerged from the analysis. However, both increases and decreases in density were more apparent towards the extreme edges of the survey area. These may represent an edge artifact of the kriging process. There was no detected effect of survey effort on our estimates of population increase. This analysis

Table 2. Moose population summary values for WMUs, Ontario, 1990–1995.

WMU	Density (moose/km^2)	Relative ranking	Area (km^2)	Population estimate
2	0.23	3.42	13 117	3029
3	0.19	4.18	12 432	2347
4	0.18	4.28	11 027	2032
5	0.30	2.65	10 745	3197
6	0.28	2.77	4 611	1313
7A	0.30	2.65	837	660
7B	0.79	1.00	9 320	2773
8	0.42	1.86	5 659	2398
9A	0.34	2.32	4 864	1653
9B	0.21	3.73	3 386	716
10	0.24	3.23	2 881	703
11A	0.38	2.09	7 704	2431
11B	0.32	2.50	2 002	755
12A	0.33	2.36	4 331	1381
12B	0.32	2.47	6 176	2065
13	0.14	5.72	12 613	1740
14	0.28	2.86	435	120
15A	0.23	3.45	10 258	2347
15B	0.26	3.07	17 065	4382
16A	0.06	13.99	17 176	968
16B	0.05	14.76	10 415	789
16C	0.08	10.42	11 331	605
18A	0.06	13.30	8 703	847
18B	0.10	8.11	11 082	657
19	0.14	5.72	10 477	1444
20	0.13	5.87	4 834	650
21A	0.18	4.43	14 559	2592
21B	0.21	3.83	13 654	2815
22	0.25	3.17	8 995	2240
23	0.19	4.26	9 341	1730
24	0.08	9.30	18 942	1607
27	0.19	4.07	9 029	1751
28	0.28	2.77	10 177	2897
29	0.28	2.84	8 068	2242
30	0.25	3.13	13 582	3423
31	0.16	4.93	10 176	1629
32	0.31	2.54	11 615	3612
33	0.22	3.59	6 506	1430
34	0.35	2.24	2 044	721
35	0.26	3.08	9 836	2520
36	0.22	3.64	6 022	1303
37	0.17	4.73	5 505	918
38	0.19	4.20	11 285	2120
39	0.27	2.90	6 154	1674
40	0.32	2.50	9 956	3143
41	0.35	2.25	9 732	3408
42	0.18	4.44	7 746	1377
43A	0.13	6.15	2 909	344
43B	0.12	6.67	176	23
46	0.13	6.13	2 376	306
47	0.13	6.13	5 374	692
48	0.24	3.25	3 983	968
49	0.12	6.56	3 623	436
50	0.36	2.18	1 779	643
51	0.48	1.64	7 112	3419
53A	0.12	6.49	2 246	273
54	0.42	1.88	1 861	781
55A	0.39	2.01	1 201	472
56	0.12	6.48	2 463	300
57	0.13	6.11	1 889	244
60A	0.02	37.39	4 201	89
61	0.10	7.99	2 489	246

Table 3. Values of κ comparing density maps based on reduced data versus all data.

Data model	κ	Var(κ)	95% confidence limit	
			Lower	Upper
25%	0.378126	6.6×10^{-6}	0.373	0.383
50%	0.500325	5.4×10^{-6}	0.496	0.505
75%	0.716013	4.2×10^{-6}	0.712	0.720

Note: Population maps had six density classes, with intervals of 0.4 moose/km^2 (see Fig. 3).

Table 4. Comparison of mean moose density (provincial level) based on an average density of 53 WMUs.

% of data included	Mean density	SE of the mean	95% confidence limit	
			Lower	Upper
100	0.2380	0.0167	0.2044	0.2715
75	0.2462	0.0170	0.2122	0.2803
50	0.2499	0.0196	0.2105	0.2892
25	0.2466	0.0170	0.2125	0.2806

Note: Means are derived from density maps using 25–100% of available moose survey points. There were no differences between means (F = 0.0836, df = 3,209, P = 0.9689). Average density in this table is based on the 53 WMUs that are surveyed annually and excludes those WMUs with very low density that are surveyed infrequently. Hence the value is slightly higher than the 0.209 moose/km^2 derived for the entire survey area.

Table 5. Average variance of WMU density from the full-data model.

% of data used	Mean variance from full-data model[a]
75	0.0097
50	0.0307
25	0.0268

Note: WMU density was derived from density maps based on 75–25% of the original survey points; lower variance indicates greater precision with the full-data model.

[a] Variance = $\sum_i (D_{\mathrm{fd}_i} - D_{\mathrm{rd}_i})^2/n$, where i = 1–53 WMUs, D_{fd_i} is the WMU density of the full-data model, D_{rd_i} is the WMU density of the reduced-data model, and n is the total number of WMUs.

supports a previous study evaluating accuracy of moose survey methods in randomized resurvey plots, where differences in time spent on plot accounted for only 6% of variance in estimated moose density (Bisset and Rempel

1991). Although increased survey effort may have elevated moose density estimates after 1986, this effect cannot explain all the spatial and temporal variance seen in our moose density maps. For example, survey effort was most consistent across years in the far northwestern region of the province (e.g., WMUs 7B and 8), yet the maps reveal that moose density increases were among the highest here.

The cause of density change, however, is not straightforward and is the focus of other research studies (e.g., Rempel et al. 1997). A selective harvest system to regulate and reduce hunting pressure was introduced in the province in 1983 (Timmermann and Whitlaw 1992; Timmermann and Rempel 1998), and timber management guidelines to provide moose habitat through logging operations were introduced between 1983 and 1986 (Ontario Ministry of Natural Resources 1988). Some combination of these factors, including interactions with environmental variables, may explain population increases. For example, the increase in moose density in the Algonquin Park area (WMU 51) may in part be related to a landscape-level shift in forest age structure and a subsequent shift from suitable deer to suitable moose habitat. Moose densities have also increased markedly in areas with pockets of highly productive clay plains (e.g., WMUs 28, 40, and 41 in the northeast and WMU 5 in the northwest).

The kriging results illustrate, in relatively fine detail, the spatial variation of moose density in these areas. These new models may help us understand the effects of environmental and biotic interactions on moose populations. For example, analysis of these landscape-level change data in relation to factors such as density of caribou and wolf populations, hunter effort, climate, soils, vegetation disturbance, and road expansions may increase our understanding of the myriad of factors limiting and (or) regulating moose populations.

At the aggregate level, our results are similar to traditional methods of calculating moose density. This suggests that the kriging approach is reliable and effective, but kriging has a clear advantage in its finer spatial resolution. Traditional methods generate population estimates for WMUs, which average 3134 km^2 within the moose range of Ontario, whereas our approach has generated density estimates on a regular grid. While the intrinsic resolution of the moose density estimates is based on 25-km^2 survey plots, a 1-km^2 visualization results in an effective resolution of about 125 times less than the average area of a WMU. The optimal resolution is the subject of ongoing research.

Our estimates of moose density are independent of the administrative unit under which the data collection was originally organized. This is useful for both spatial and time series analysis of population trends. WMUs in Ontario have been reorganized at least twice in the past 20 years, making time series analysis difficult as unit boundaries change, but the kriging method is unaffected by reorganization of boundaries. Artificial administrative boundaries conceal spatial trends among units, making it more difficult to identify geographical trends. Lumping data within an administrative unit may also serve to conceal relationships between density and environmental factors at scales below the administrative unit. Density calculation based on discrete administrative units is also insensitive to density of neighbouring units, and therefore, estimates cannot be statistically improved by knowledge of density in the adjacent unit.

Our analysis of reduced sample sizes, by removing one, two, or three of every four data points and then recalculating moose densities, was somewhat limited because a “jackknife” approach, where all permutations of the data are evaluated, was not used. Nonetheless, it did provide a first approximation of the possible impact of reducing sample rate. The issue is not trivial. For example, in 1995–1996, helicopter time costs were approximately Can$300/h for ministry aircraft. Each survey flight takes approximately 79 min (including ferry time), resulting in an average cost of $395 per plot (Bisset et al. 1997). With reduced budgets, fewer staff, and changing priorities, reducing the cost of obtaining reliable wildlife density estimates is very important. We found that at both the provincial and WMU levels, reducing sample rate increased error in the density estimate. In both cases, however, this difference was relatively minor at the 75% sampling level, but error increased markedly when only 50 or 25% of the original data were used to estimate density.

The results suggest that the current intensity of Ontario Ministry of Natural Resources moose surveys is reasonably robust for estimating 5-year averages of moose density, as removing one of every four points has a relatively small effect on the estimates. Reducing survey intensity by an amount >25% has a more significant destabilizing effect, causing a decrease in both accuracy and precision. An important implication is that a single year’s survey is undoubtedly insufficient to estimate moose populations at almost any scale without large confidence limits, but this is the subject of additional research.

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References

Bisset, A.R. 1991. Standards and guidelines for moose aerial inventory in Ontario. Ontario Ministry of Natural Resources, Toronto, Ont.

Bisset, A.R., and McLaren, M.A. 1995. Moose population inventory plan for Ontario, 1996–1998. IR-02. Ontario Ministry of Natural Resources, Thunder Bay.

Bisset, A.R., and Rempel, R.S. 1991. Linear analysis of factors affecting the accuracy of moose aerial inventories. Alces, **27**: 127–139.

Bisset, A.R., McLaren, M., Edmonds, C., Sawyer, W., Gluhushkin, W., Morrison, K., and Davies, C. 1997. Report on the 1995–96 and 1996–97 moose population surveys: with considerations for future surveys. TR-113. Ontario Ministry of Natural Resources, Thunder Bay.

Boyer, D.G., Wright, R.J., Feldhake, C.M., and Bligh, D.P. 1996. Soil spatial variability relationships in a steeply sloping acid soil environment. Soil Sci. **161**: 278–287.

Congalton, R.G. 1991. A review of assessing the accuracy of classifications of remotely sensed data. Remote Sens. Environ. **37**: 35–46.

Congalton, R.G., and Mead, R.A. 1983. A quantitative method to test for consistency and correctness in photointerpretation. Photogramm. Eng. Remote Sens. **49**: 69–74.

Congalton, R.G., Oderwald, R.G., and Mead, R.A. 1983. Assessing Landsat classification accuracy using discrete multivariate analysis statistical techniques. Photogramm. Eng. Remote Sens. **49**: 1671–1678.

Crête, M. 1989. Approximation of *K* carrying capacity for moose in eastern Quebec. Can. J. Zool. **67**: 373–380.

Davis, J.S., McKenney, D.W., and Turnbull, J.W. 1994. The international impact of forestry research and a comparison with agricultural and fisheries research. Can. J. For. Res. **24**: 321–336.

Deutsch, C.V., and Journel, A.G. 1992. GSLIB: geostatistical software library and user's guide. Oxford University Press, New York.

Donald, W.W. 1994. Geostatistics for mapping weeds, with a Canada thistle (*Cirsium-arvense*) patch as a case study. Weed Sci. **42**: 648–657.

Gribko, L.S., Liebhold, A.M., and Hohn, M.E. 1995. Model to predict gypsy moth (Lepidoptera, Lymantriidae) defoliation using kriging and logistic regression. Environ. Entomol. **24**: 529–537.

Halvorson, J.J., Smith, J.L., Bolton, H., and Rossi, R.E. 1995. Evaluating shrub-associated spatial patterns of soil properties in a shrub–steppe ecosystem using multiple-variable geostatistics. Soil Sci. Soc. Am. J. **59**: 1476–1487.

Hammond, T., and Yarie, J. 1996. Spatial prediction of climatic state factor regions in Alaska. Ecoscience, **3**: 490–501.

Heisel, T., Andreasen, C., and Ersboll, A.K. 1996. Annual weed distributions can be mapped with kriging. Weed Res. **36**: 325–337.

Holdaway, M.R. 1996. Spatial modeling and interpolation of monthly temperature using kriging. Clim. Res. **6**: 215–225.

Isaaks, E.H., and Srivastava, R.M. 1989. An introduction to applied geostatistics. Oxford University Press, New York.

Krebs, C.J. 1984. Ecology: the experimental analysis of distribution and abundance. Harper and Row, New York.

Maravelias, C.D., and Haralabous, J. 1995. Spatial distribution of herring in the Orkney Shetland area (northern North Sea)—a geostatistical analysis. Neth. J. Sea Res. **34**: 319–329.

MathSoft Inc. 1996. S+Spatialstats user's manual, version 1.0. MathSoft Inc., Seattle, Wash.

Maynou, F., Conan, G.Y., Cartes, J.E., Company, J.B., and Sarda, F. 1996. Spatial structure and seasonality of decapod crustacean populations on the northwestern Mediterranean slope. Limnol. Oceanogr. **41**: 113–125.

Naesset, E. 1996. Use of the weighted kappa coefficient in classification error assessment of thematic maps. Int. J. Geogr. Inf. Syst. **10**: 591–604.

Odeh, I.O.A, Mcbratney, A.B., and Chittleborough, D.J. 1994. Spatial prediction of soil properties from landform attributes derived from a digitial elevation model. Geoderma, **63**(3–4): 197–214.

Olea, R. 1991. Geostatistical glossary and multilingual dictionary. Oxford University Press, New York.

Ontario Ministry of Natural Resources. 1988. Timber management guidelines for the provision of moose habitat. Ontario Ministry of Natural Resources, Toronto.

Rempel, R.S., Elkie, P.C., Rodgers, A.R., and Gluck, M.J. 1997. Timber-management and natural-disturbance effects on moose habitat: landscape evaluation. J. Wildl. Manage. **61**: 517–524.

SAS Institute Inc. 1989. SAS/STAT user's guide, version 6, edition 4. SAS Institute Inc., Cary, N.C.

SAS Institute Inc. 1996. SAS/STAT software. Changes and enhancements through release 6.11. SAS Institute Inc., Cary, N.C.

Timmermann, H.R., and Rempel, R.S. 1998. Age and sex structure of hunter harvested moose under two harvest strategies in north central Ontario. Alces, **34**: 21–30.

Timmermann, H.R., and Whitlaw, H.A. 1992. Selective moose harvest in north central Ontario—a progress report. Alces, **28**: 137–163.

Villard, M., and Maurer, B.A. 1996. Geostatistics as a tool for examining hypothesized declines in migratory songbirds. Ecology, **77**: 59–68.

Weseloh, R.M. 1996. Developing and validating a model for predicting gypsy moth (Lepidoptera, Lymantriidae) defoliation in Connecticut. J. Econ. Entomol. **89**: 1546–1555.

Whitlaw, H.A., Timmerman, H.R., Pernsky, P., and Bisset, A.R. 1993. Northwest region moose population and harvest profile. TR-75, NWST, Ontario Ministry of Natural Resources, Thunder Bay.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Englewood Cliffs, N.J.