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SPATIAL DESCRIPTION AND ANALYSIS OF GRASS-HOPPER ABUNDANCES IN COLORADO RANGELAND

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ABSTRACT—Although rangeland grasshopper populations have been studied for more than 120 years, little is known of the spatial patterns in grasshopper numbers between outbreak cycles. This information is necessary to understand how grasshopper outbreaks develop and to correctly design research, monitoring, and modeling projects. We used exploratory data analysis and geostatistics to identify the spatial patterns in grasshopper numbers for 1993 through 1997 in Colorado. The same family of models (spherical) provided the best fit to the sample data for all years, which implies that similar processes influenced grasshopper densities over these years. The parameters of the models differed among years, however, which suggests that the scale of spatial patterning changed over time. Since Colorado grasshopper densities were patterned at scales larger than those reported for other areas of the Great Plains, our results suggest that survey methods for Colorado are not adequate to identify small-scale "hot spots" of high grasshopper numbers, inhibiting prediction of potential outbreak foci in this region.

Introduction

> A cloud was over the sun. . . . The cloud was grasshoppers. Their
> bodies hid the sun and made darkness. Their thin, large wings
> gleamed and glittered. The rasping whirring of their wings filled
> the whole air and they hit the ground and the house with the noise
> of a hailstorm.
>   —Laura Ingalls Wilder, *On the Banks of Plum Creek* (1937)

This passage from Laura Wilder's journal describes her first encounter
with the Rocky Mountain locust, *Melanoplus spretus* (Walsh), a devastating
pest of early western farms and rangeland. Despite the extinction of this
species in the early 20th century, high numbers of grasshoppers, commonly
called outbreaks, have continued periodically to cause major economic
losses to rangelands throughout the Great Plains. After more than 120 years
of research on the grasshopper problem, our understanding of rangeland
grasshopper population dynamics is still incomplete (Skinner 2000). We
cannot predict accurately when or where the next grasshopper outbreak will
occur, and we do not know precisely what factors contribute to the develop-
ment of high grasshopper densities.

As with any pest, the cost of intervention is lowest at early stages in the
grasshopper outbreak cycle, when populations are building up but do not yet
impact large areas. Detection of high population densities at early stages is
crucial for early intervention to minimize grasshopper damage. Early detec-
tion requires sampling schemes that are aimed at determining the risk of
high grasshopper numbers, increasing readiness for intervention, and pin-
pointing the locations where outbreaks are likely to occur. Additionally,
surveys of grasshopper populations can locate "hot spots" of activity, where
rising densities may indicate a developing problem. Since 1934, the US
Department of Agriculture's Animal and Plant Health Inspection Service
has funded grasshopper management efforts on rangeland (USDA 1982). To
enhance the effectiveness of control, grasshopper surveys have been con-
ducted regularly over most of the western United States; however, decreas-
ing federal funds for these efforts have reduced the frequency of sampling
over both time and space. To extract the most insights and information from
these publicly funded surveys, the sampling should be done at a spatial scale
that best captures the pertinent information about grasshopper population
dynamics at low, moderate, and high densities.

While studies of the spatial and temporal development of grasshopper outbreaks have been conducted for several parts of North America (Cigliano et al. 1995; Lockwood and Schell 1995; Schell and Lockwood 1997), little is known about grasshopper populations in the Great Plains under non-outbreak conditions (but see Przybyszewski and Capinera 1990). Understanding the distribution of grasshopper abundances, through description and analysis of their spatial patterns, is essential to understanding the processes that produce the distribution (Allen and Hoekstra 1992; Chou 1993). Examination of patterns of grasshopper abundance also holds promise for elucidating the factors involved in the initiation, development, and subsidence of outbreaks. In addition, analysis of spatial patterns in low-level endemic grasshopper densities can aid in identifying habitats prone to producing high densities and help to assess the adequacy of current survey methods for detecting infestations that are likely to spread. Toward these ends, we conducted spatial analyses to (1) identify patterns of grasshopper abundances in Colorado, (2) quantify the spatial scale of those patterns, and (3) determine the adequacy of current grasshopper survey techniques for detecting both large-scale (regional) and small-scale (field-size) infestations.

Methods of detecting and describing spatial patterns developed in the field of geology have recently been applied to ecological phenomena. These methods are collectively referred to as geostatistics or spatial statistics. Geostatistical methods, such as variography, have been used to show how grasshopper abundances differ between years in Idaho (Fielding and Brusven 1993) and across environmental regions of Montana (Kemp et al. 1989). Johnson and Worobec (1988) reported on the spatial autocorrelation, the degree to which neighboring values are correlated, in grasshopper densities in Alberta, Canada. Spatial statistics have also been used to produce grasshopper hazard maps via kriging, which uses values of nearby spatial locations to estimate values at unsampled locations (Kemp et al. 1989). However, none of these applications reported conducting the supporting exploratory data analyses necessary for accurate ecological interpretation of spatial patterns and to guide subsequent analyses (Rossi et al. 1992).

In this study, we report the exploratory data analysis used to determine whether grasshopper densities from five years exhibited spatial patterning. We used two geostatistical methods, Moran's I statistic and variography, to determine and test the scale of spatial dependence among grasshopper counts. Our results show that Colorado grasshopper densities are spatially autocorrelated, so densities in one area may be used to predict densities in another, but at scales larger than have previously been reported. Such large-

scale patterning in grasshopper abundances in nonoutbreak years has impli-
cations for the design of survey and modeling tools necessary to predict, and
potentially prevent, future outbreaks.

Materials and Methods

Grasshopper Data

As part of their Cooperative Agricultural Pest Survey, the US Depart-
ment of Agriculture's Animal and Plant Health Inspection Service-Plant
Protection and Quarantine (APHIS-PPQ) unit coordinates annual surveys of
adult grasshoppers to produce state and national outlook maps with esti-
mates of the next year's populations (USDA 1982, 1987). Until 1995, the
survey sampled sites at 5-mile intervals throughout Colorado grasslands.
More recently, fewer than 150 representative rangeland sites have been
visited each year, although many of the same sites are revisited year after
year. The goal of these surveys is to monitor grasshopper densities and
determine the likelihood that populations will reach numbers high enough
to cause economic damage and require treatment. Each site in the survey is
sampled by making 50 visual checks for presence of one or more grasshop-
pers in a 0.1 m^2 area (E. Danielson-Buffington, Colorado State University,
personal communication). Grasshopper densities are then estimated using
the Poisson probability density function (Onsager 1991; Legg et al. 1993).

The US Department of Agriculture grasshopper survey data for 1993
through 1997 were acquired in digital form and inspected for outliers, data
that do not correspond with other samples and are usually a result of
transcription errors or are otherwise inconsistent with the remainder of the
data. One site each in 1995 and 1997 was reported to have a longitude near
120° W. Because these values would put the sites outside Colorado, the
longitudes were likely erroneous and the sites were removed. Grasshopper
densities were also inspected, and two sites with questionably high densities
(approx. 200 grasshoppers per yd^2) were removed from the 1996 data set.
Densities were converted to numbers per m^2 where necessary.

The locations for sites sampled in 1994 were recorded in the Universal
Transverse Mercator system, which minimizes distortion of area, distance,
and direction. Locations for all other years were recorded in latitude and
longitude but were transformed to the Universal Transverse Mercator sys-
tem meters for zone 13 using PC ARC/INFO 3.5.1 (ESRI 1997), and all
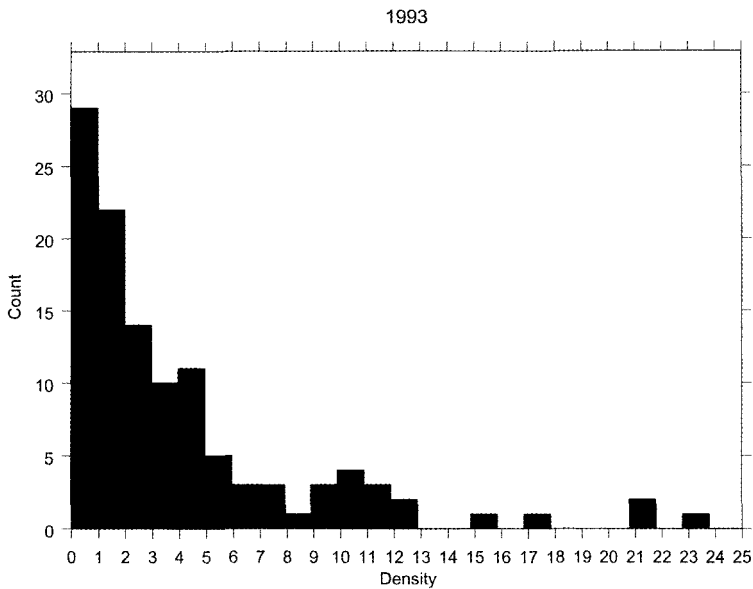analyses were performed using these location coordinates.

1993

Figure 1. Representative histogram of Colorado grasshopper densities (number per m^2) for 1993, showing the general pattern of many zero or low values and few high values.

Exploratory Data Analyses

Various techniques were used to detect and describe spatial patterns in Colorado grasshopper densities. Summary univariate statistics and standard two-sample t-tests between means were performed to determine whether differences existed in grasshopper densities between years. To assess the sampling distribution of the grasshopper data, frequency histograms were made for each year's densities. These histograms showed that the grasshopper densities were positively skewed in all years sampled (e.g., Fig. 1), with many zero or low values and few high values. For better approximation to the normal distribution, a ln(density + 1) transformation was performed before proceeding with the spatial analyses.

We used data posting as a simple visual tool for spatial display and description (Isaaks and Srivastava 1989). In data posting, a map of data values was made by plotting the grasshopper density of each site as the display symbol (Fig. 2). Examination of the plotted data reveals the highest
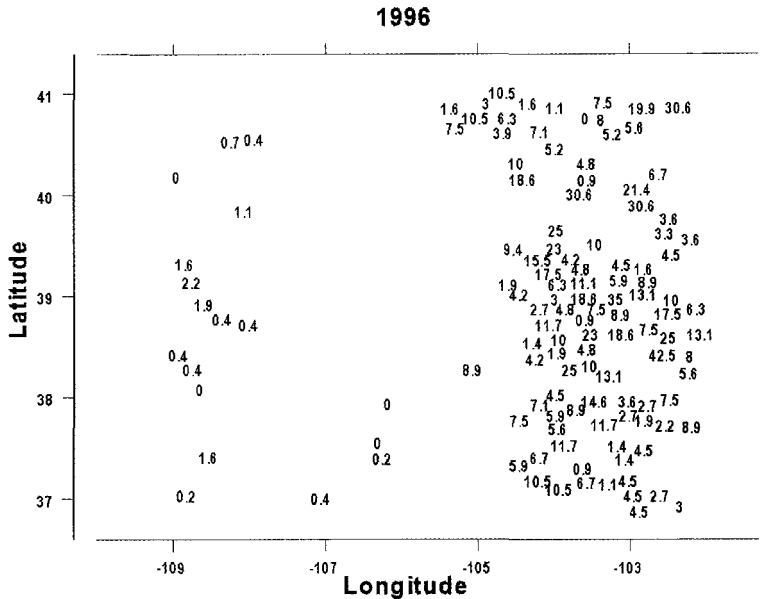
1996

Figure 2. Representative posted grasshopper densities (number per m²) for 1996, showing the general pattern of occurrence. Some sites have been moved or omitted for legibility.

and lowest values, trends, and outliers. If similar values map close together, there may be spatial dependence in the plotted variable. Data posting can also show patterns in how data were collected, since areas of interest may be represented by more samples.

We also used bivariate scatterplots as a way to display our spatial data. The data were graphed with one axis corresponding to grasshopper densities and the other axis corresponding to a locational coordinate, i.e., either latitudinal or longitudinal coordinates (Rossi et al. 1992; Isaaks and Srivastava 1989). Such scatterplots were used to look for a nonrandom distribution of the data and to check for outliers. Bivariate scatterplots of grasshopper density by longitude and latitude were examined to reveal spatial trends and give visual clues to the presence and direction of spatial dependence.

Geostatistics

The assumption underlying the use of conventional parametric statistical methods is that the data are independent and identically distributed. Unfortunately, these assumptions are violated when the data are spatially or temporally correlated. This is often the case for ecological data, where samples taken close to one another are more similar than samples taken farther apart (Rossi et al. 1992). This phenomenon is variously referred to as spatial dependence, spatial continuity, or spatial autocorrelation. Alternative statistical tools are needed when dealing with autocorrelated data. A body of such tools, collectively known as geostatistics, has been developed in the field of geology, and subsequently applied in ecology, for modeling spatial dependence. Geostatistical tools include tests for spatial autocorrelation, *h*-scattergrams, variograms, correlograms, and kriging (Rossi et al. 1992). The spatial analysis functions used here were provided by Reich and Davis (1998) and were performed in S-PLUS 4.0 for Windows (MathSoft 1997).

Spatial Autocorrelation. Spatial autocorrelation is the degree to which the value of a variable at a given sampled site is correlated with the values for the same variable at neighboring sites (Sokal and Oden 1978a). Positive spatial autocorrelation produces a pattern where sites of similar values tend to be adjacent and negative autocorrelation indicates that sites with similar values are dispersed (Chou 1993). When there is no significant spatial autocorrelation, the pattern is random. Tests for spatial autocorrelation include a number of indices that measure the degree to which values of a variable are correlated with each other, the most common of which is Moran's I statistic (Moran 1950). Moran's I is analogous to a correlation coefficient; it ranges between -1 and 1, with the sign indicating whether the spatial correlation is positive or negative. The statistic is calculated under the null hypothesis of spatial independence (no spatial autocorrelation) as:

$$I = \frac{n \sum\limits_{i=1}^{n}\sum\limits_{j=1}^{n} \delta_{ij}\,(Z_i - \bar{Z})(Z_j - \bar{Z})}{2A \sum\limits_{i=1}^{n}(Z_i - \bar{Z})^2}$$

where n is the number of sampled points; 2A is $\sum\sum \delta_{ij}$, the total number of pairs of points; δ_{ij} is a matrix of weights based on the inverse distance

between the ith and jth points; and Z_i is the observed value of the variable of interest at the ith sampled point (Cliff and Ord 1973; Chou 1993). The expected value of Moran's I under the null hypothesis of no spatial autocorrelation is determined from the spatial weights matrix of the data. The difference between the observed and expected values of I is tested for significance.

Moran's I was calculated for natural log-transformed grasshopper densities, which more closely approximated the standard normal distribution assumed in hypothesis testing (Cliff and Ord 1973; Ord 1979; see also Sokal and Oden 1978a). P-values for I were calculated for 500 random permutations of the data, and the test statistic was rescaled so that each row of the spatial weights matrix δ_{ij} summed to 1. Moran's I tests were performed separately within each sampled year, once using all sites and once using only the eastern Colorado shortgrass sites. Moran's I was also calculated for increasing distances around sample points and summed to find the cumulative value of I for each distance class (0-0.1 km, 0.1-0.25 km, . . . , 1-2.5 km, . . . , 10-20 km, . . . , 400-500 km). This cumulative value of the I statistic can be graphed against the distance classes to identify the scale of autocorrelation (Reich et al. 1994; see also Greig-Smith 1952). If the cumulative value of I decreases with increasing distance, the spatial pattern is one of regularly distributed patches. The plot of cumulative I against distance will reach an asymptote when patches are aggregated or randomly distributed (Reich et al. 1994). The distance at which the curve levels off indicates the scale of the spatial pattern (R. Reich, Colorado State University, personal communication). The peak of the cumulative value of Moran's I is analogous to the range for the sample variogram, and it can be expected to have a similar value.

Variography. We applied a method that is traditionally used to describe and quantify spatial autocorrelation, called the variogram or semivariogram. A variogram summarizes the degree of similarity between data values, for all possible pairings of the data, as a function of the distance between the samples (Rossi et al. 1992; Liebhold et al. 1993). The sample variogram is calculated as:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [z(x_i) - z(x_i + h)]^2$$

where $\gamma(h)$ is the semivariance for lag distance h, $N(h)$ is the number of pairs of sampled points separated by h, and $z(x_i)$ is the observed data value at location x_i (Rossi et al. 1992).

Several characteristics of the variogram are used to describe its structure. The value at which the variogram levels off is known as the sill and is equivalent to the sample variance. The distance at which the variogram reaches the sill is called the range; this represents the average distance at which samples are spatially autocorrelated (Isaaks and Srivastava 1989; Rossi et al. 1992; Liebhold et al. 1993). Thus, the range is analogous to the asymptote of the cumulative plot of Moran's I statistic.

The value of the variogram is strictly zero for zero distance, since there can be no variability between a sampled point and itself. In practice, however, the calculated value of the sample variogram may not be zero at very small distances, causing a discontinuity at zero called the nugget effect (Isaaks and Srivastava 1989). The positive value at which the variogram appears to intercept the ordinate is called the nugget, and it represents either sampling error or spatial variability at distances smaller than the minimum sampling distance (Rossi et al. 1992; Liebhold et al. 1993).

We calculated the sample variogram for each year's data using the spatial library for S-PLUS developed by Reich and Davis (1998). If no spatial autocorrelation was detected using Moran's I, then variography was not performed on the data set. Each variogram was calculated to about half the maximum distance between points (Liebhold et al. 1993). The nugget, range, and sill of each sample variogram were estimated and used as parameters to iteratively fit a linear, spherical, exponential, or Gaussian model to the sample variogram. Fitting a model to the sample variogram is a prerequisite for kriging, a method used to estimate values over an area, such as when constructing grasshopper density hazard maps. Although kriging is not done here, the variograms are modeled to provide insights into the patterns of spatial continuity in the data. The model with the lowest corrected Akaike Information Criterion was selected as the best fit to the sample variogram. Variogram modeling provides insights into the scales of processes that are involved in determining spatial structure (Meisel and Turner 1998). If variogram models differ substantially across years, then we can infer different patterns of variation which in turn result from different processes (Sokal and Oden 1978b).

Variograms can be calculated for all directions at once (omnidirectional variogram) or, for instance, in the north-south or east-west direction, to search for a directional trend in the data. The presence of directionality is

TABLE 1

SURVEYED COLORADO GRASSHOPPER DENSITIES

	Year				
	1993	1994	1995	1996	1997
Number (per m^2)	106	99	98	132	118
Mean	4.20	4.90	3.18	7.97	2.43
Median	2.5	2.1	1.5	5.6	1.6
Standard deviation	4.77	7.13	4.87	8.11	2.54
Minimum	0	0	0	0	0
Maximum	23.4	32.6	26.8	42.5	12.5
Interquartile range	4.20	4.50	2.00	8.23	2.60
Coefficient of variation	1.14	1.45	1.53	1.02	1.05

termed "anisotropy." Kemp et al. (1989) examined Montana grasshopper counts for anisotropy and concluded that omnidirectional variograms were appropriate for kriging purposes, the main use of variography for grasshopper densities. Accordingly, only omnidirectional variograms were computed here.

Results

Exploratory Data Analyses

The mean grasshopper density over all sites differed among years (Table 1). Densities were highest in 1996, with a median density of 5.6 grasshoppers per/m^2, more than twice that of any other year. Populations in all years averaged at or below the moderate density of eight grasshoppers per/m^2. The maximum grasshopper density observed was 42.5 grasshoppers/m^2 in 1996 and the lowest was 12.5 grasshoppers/m^2 in 1997 (Table 1).

Data posting (Fig. 2) reflected the respective histogram for each year, showing many sites with low densities scattered across the state. Areas of moderate to high densities were somewhat clustered but were also scattered amid low density sites (Fig. 2). In general, densities were low in the western

half of Colorado, and the higher densities were well dispersed among lower densities in eastern Colorado. Posting also revealed differences in sampling intensity across the state: most of the sampled sites were located in the eastern third of the state. Very few samples are taken in the middle longitudes, which correspond to the mountainous areas of the state.

Bivariate scatterplots (Fig. 3) revealed a weak relationship between density and longitude for all years, with high densities located mostly between about 104° and 102° W longitude. However, the correlations between density and locational coordinates were generally low ($r^2 < 0.4$). The paucity of sites in the western longitudes makes it difficult to determine whether this is a real trend or an artifact of unbalanced sampling.

Geostatistics

Tests using Moran's I statistic on the entire data set revealed significant positive spatial autocorrelation in all years (Table 2). When Moran's I was calculated for the sites in eastern Colorado only, significant positive autocorrelation was found in all years except 1995. Cumulative calculations of Moran's I were plotted against distance (Fig. 4). The I statistic reached a higher cumulative value in 1993 than in the other years, indicating stronger positive autocorrelation, especially over distances up to 20 km (Fig. 4). All of the curves leveled off at distances greater than 100 km, revealing spatial autocorrelation at that scale.

The best-fitting variogram model and parameter estimates for each data set in which significant spatial autocorrelation was found (Table 3) show that the model shape differed only slightly between years. For Colorado as a whole, the spherical model gave the best fit in all years. When variograms were calculated for the eastern sites only, the spherical model again gave the best fit, except in 1994 when the Gaussian model gave a slightly better fit. The parameters of the fitted variogram models differed over time (Table 3). The range, for example, varied between 60 and 125 km for the whole data set and between 25 and 160 km for eastern sites.

Discussion

During the years of this study, Colorado grasshopper populations remained at or below the traditional minimum threshold of 9.6 grasshoppers per m² for federally funded control activities (USDA 1982, 1987; Davis et al. 1992). Mean densities also remained below the regional carrying capacity of
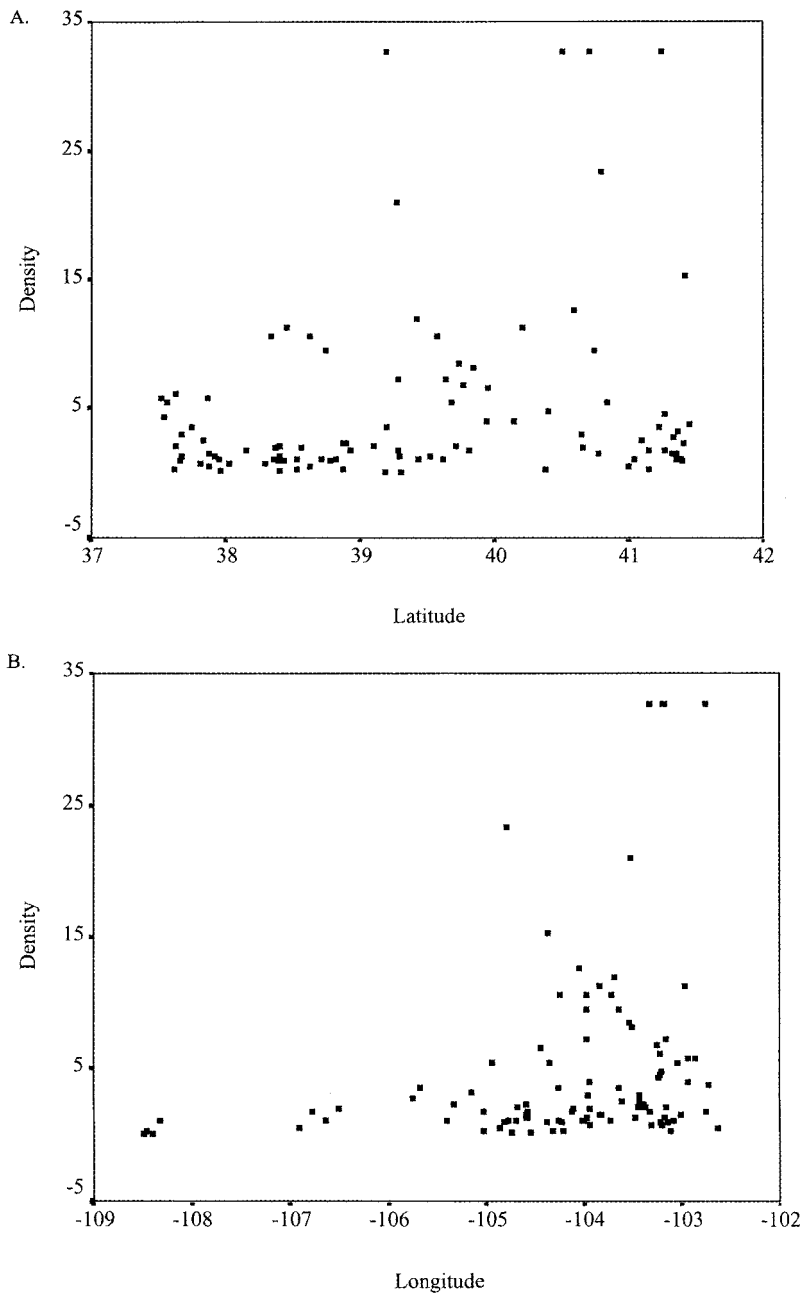
Figure 3. Representative bivariate scatterplots for 1994, showing general relationship between density (number per m²) and location. A. Density vs. latitude; B. Density vs. longitude.

TABLE 2

SPATIAL AUTOCORRELATION IN GRASSHOPPER DENSITIES USING MORAN'S I STATISTIC

	Year				
	1993	1994	1995	1996	1997
All sites					
Dimension	106	99	98	132	118
Moran's I	0.179	0.0802	0.0899	0.161	0.129
Mean of I	-0.0112	-0.00970	-0.0114	-0.00692	-0.00804
Std. Dev.	0.0370	0.0189	0.0207	0.0374	0.0165
P-value[a]	0*	0*	0*	0*	0*
Eastern Colorado sites only					
Dimension	88	91	79	113	98
Moran's I	0.232	0.0639	0.0318	0.0916	0.0694
Mean of I	-0.0133	-0.0118	-0.0131	-0.00912	-0.0103
Std Dev	0.0453	0.0211	0.0208	0.0467	0.0164
P-value[1]	0*	0.008*	0.056	0.036**	0*

Note: Based on 500 random permutations of the data. The mean and standard deviation of I are calculated under the null hypothesis of no spatial autocorrelation.
[a] Two-sided test on log-transformed densities
* Significant at $\alpha = 0.01$ level
** Significant at $\alpha = 0.05$ level

8.6 to 8.9 grasshoppers per m^2 calculated by Kemp and Dennis (1993) for plains regions of Montana, although the carrying capacity for grasshoppers on Colorado rangeland may be expected to differ from that of Montana due to differences in the species composition of their grasshopper and plant communities (Skinner 1995). In any case, grasshopper densities were clearly at non-outbreak levels, and they did not appear to be building toward any impending problem (Table 1). Further study will be needed to compare the spatial patterns detected here with patterns in years when densities are at different stages in the outbreak cycle.
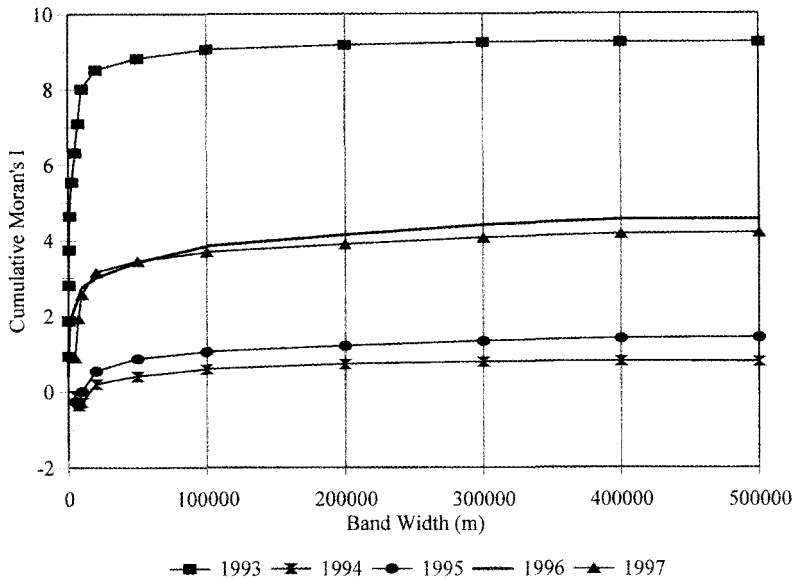
Figure 4. Cumulative values of Moran's I statistic plotted against distance.

Data posting showed a higher density of sampling sites in the eastern half of Colorado (Fig. 2), implying greater interest in monitoring grasshopper populations on the shortgrass steppe than in the western plateaus. The distribution of sampling sites is probably the result of historical outbreak frequencies, differences in land use, and the investment in agricultural productivity. Higher grasshopper densities in the eastern plains were scattered among sites with very low densities, resulting in only a weak relationship between density and longitude (Figs. 2 and 3). Drier climatic conditions on the eastern plains of Colorado would generally favor grasshopper populations (Gage and Mukerji 1977; Capinera and Sechrist 1982); however, it is unclear whether the trend in this direction in the bivariate scatterplots is a real relationship or an artifact caused by the paucity of sites in the western half of the state. Nonetheless, exploratory data analysis did suggest spatial autocorrelation in the data, and thus supported subsequent use of geostatistics to quantify the scale and pattern of that autocorrelation.

Calculation of Moran's I statistic showed that the spatial autocorrelation in grasshopper densities was positive (Table 2), indicating an aggregated, patchy pattern of occurence. As expected from the posted data

TABLE 3

SPATIAL DEPENDENCE IN COLORADO GRASSHOPPER
POPULATIONS, MEASURED BY CUMULATIVE VALUES OF
MORAN'S I STATISTICS AND VARIOGRAPHY

Data set	Year				
	1993	1994	1995	1996	1997
All sites					
Peak[a] (km)	20	300	400	400	400
Value[a] at peak	8.5	0.80	1.4	4.5	4.2
Variogram model	Spherical	Spherical	Spherical	Spherical	Spherical
Nugget	0.214	0.164	0.163	0.231	0.124
Range (km)	125	60	100	70	60
Sill	0.548	0.705	0.592	0.614	0.355
Eastern Colorado sites					
Variogram model	Spherical	Gaussian	Spherical	Spherical	Spherical
Nugget	0.235	0.140	0.134	0.261	0.106
Range (km)	160	25	75	60	50
Sill	0.551	0.706	0.598	0.605	0.345

[a] For cumulative Moran's I

map, autocorrelation was found for all years across Colorado as a whole but not when only the eastern half of the state was examined, reflecting the scattered distribution of higher density sites among lower density sites in the eastern shortgrass region. Limiting the analysis to the sites on the eastern plains reduced the size of the study area, which, as Turner et al. (1989) have shown, reduces the ability to detect "rare" patches, such as those few sites at which high grasshopper densities were found (Fig. 1). However, these hot spots are exactly the patches of interest in surveying grasshopper populations. Thus, although the grasshopper communities of the eastern plains are the ones that typically develop problematic densities, surveys covering the

state as a whole provide the best information on incipient problems when analyzed with the techniques used here.

Although the specific characteristics of the spatial structure varied among years, the data were similar enough across those years to be modeled by the same family of variogram models (Table 3). It may be that the same processes influenced grasshopper densities and their spatial patterns over the five years studied. However, similar patterns can be generated by different processes (Lawton 1999), and identical correlograms can result from different patterns of variation (Sokal and Oden 1978b). Thus, variography indicates the scale at which ecological processes impact patterns in grasshopper densities, but does not allow one to determine whether the same suite of mechanisms were involved across these non-outbreak years, let alone between non-outbreak and outbreak years.

Comparison of the fitted variograms with those of previous studies is problematic. The work of Fielding and Brusven (1993) in Idaho fitted only exponential models, while Kemp et al. (1989) fitted only spherical models, so comparison based on the shape of the best fitting model is not possible. The spatial structure (e.g., sill and nugget values) is also difficult to compare unless variograms are standardized (Rossi et al. 1992), although ranges may be directly compared. Our ranges (Table 3) are comparable to those of Johnson (1989; Johnson and Worobec 1988), who found significant positive spatial autocorrelation to distances of 20-50 km for grasshopper populations in Alberta, and to those of Kemp et al. (1989), who calculated ranges of 43-112 km for Montana. However, Fielding and Brusven (1993) reported shorter ranges (14 to 53 km) for a smaller study area (15,000 km^2) in Idaho.

The two geostatistical methods used to determine the scale of spatial autocorrelation in grasshopper densities varied in their results. While the range represents the average distance to which data are spatially autocorrelated (Rossi et al. 1992), these ranges did not match the peaks of the cumulative Moran's I plots. The cumulative values of Moran's I statistic suggested that the largest scale of spatial patterning to be on the order of more than a hundred kilometers (Fig. 4), while the variogram suggested ranges between 25 and 160 km (Table 3). However, larger scales of patterning are apparent even in the variograms, as the semivariance increased above the sill for the largest lag distances (Fig. 5). These larger patterns in grasshopper density can only be detected by sampling grasshopper densities in both Colorado and adjacent states. Indeed, Capinera and Horton (1989) found that infestation levels may be positively correlated between adjacent states, although this effect may be due to the tendency for contagion to
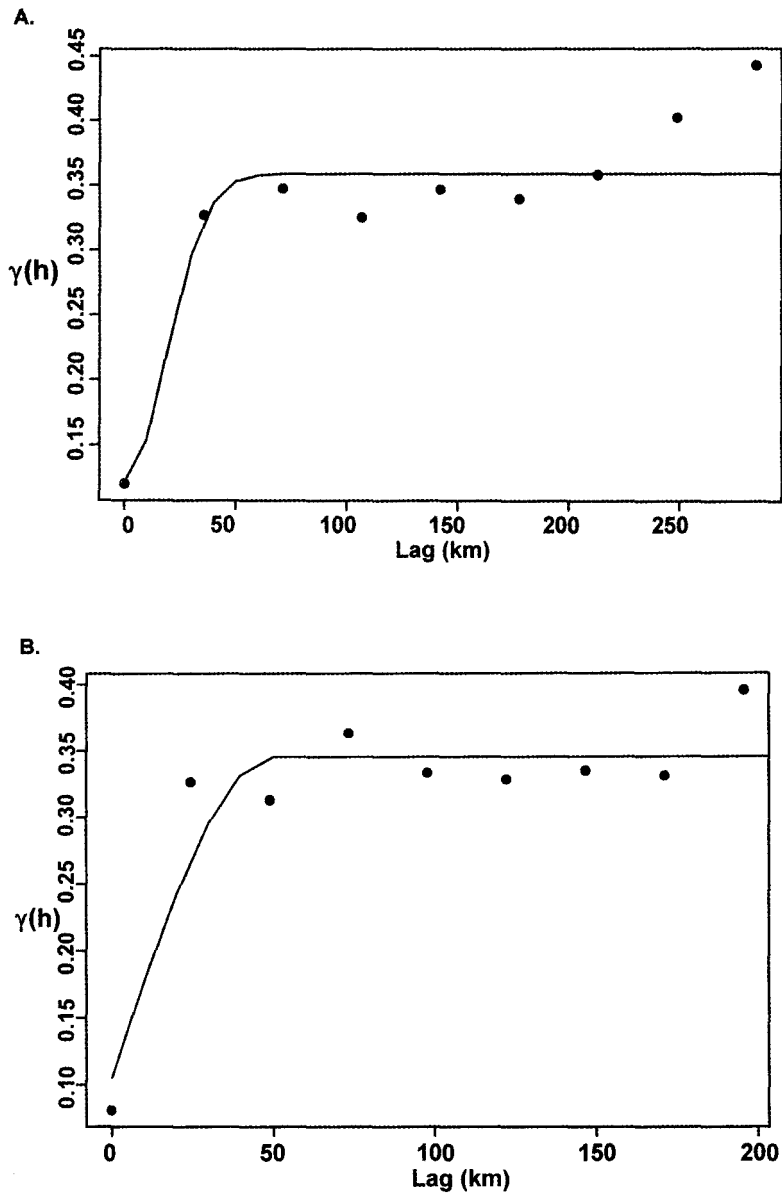
A.

B.

Figure 5. Representative variograms for 1997 grasshopper densities (number per m²).
The y-axis represents the semivariance for the lag distance given on the x-axis.
A. All sites; B. Eastern Colorado sites only.

increase with the extent of area sampled (Turner et al. 1989). Nonetheless, characterization of spatial patterning in grasshopper abundances at a larger, regional scale would help to identify and understand potential regional outbreak patterns. Regional data collection would provide the greatest insights into grasshopper dynamics if the samples taken were coordinated across states rather than "scaled up" to show the regional landscape pattern (see Skinner 2000).

The lack of strong evidence for spatial autocorrelation at smaller scales may be explained by one of the following causes. First, Moran's I statistic is chiefly used to detect presence and direction of spatial autocorrelation, not the scale of such patterning. The cumulative sum of Moran's I over increasing distances can indicate the largest scale at which patches are aggregated; however, grasshopper densities may exhibit spatial patterns at multiple scales which may be nested, such that autocorrelation at smaller scales is masked by patterns at larger scales. A second explanation may be the relatively small number of sites sampled over the years of this study (about 100 samples in each year). More than a thousand sites were sampled over a 200,000 km^2 area for Johnson and Worobec's (1988) calculations, and more than 400 sites were used by Kemp et al. (1989) in computing variograms for Montana's plains. The smaller number of samples for a comparable spatial area (267,000 km^2) results in poorer resolution, so changes in grasshopper densities at scales of less than 50 km may be present but not detected. Also, this effect may be caused by the low to moderate population levels in the years sampled. When grasshopper densities are high, populations show strongly clumped patterns. Infestations are not uniformly distributed across suitable habitat but instead form "hot spots" of high densities (Schell and Lockwood 1997). At the lower densities seen here, however, autocorrelation is less pronounced. The frequency distribution of the data (Fig. 1) also may have influenced the results of Moran's I statistic. Even the log-transformed data were positively skewed, and the few sites with high densities may have "dominated the lattice," violating the assumption that the statistic is asymptotically normal (Cliff and Ord 1973; Ord 1979).

These results, suggesting the large-scale patterning of Colorado grasshopper populations, have implications for pest management. Lockwood and Schell (1995) found that hot spots, small areas where grasshopper densities exceed 9.6 individuals/m^2, averaged 8.2 km^2 in size in Wyoming. They recommended treatment of such hot spots when they exceeded 2.5 km^2 in area and persisted for more than two years, because such localized areas of

high densities tend to persist and expand if left untreated. Unfortunately, the federally funded surveys conducted in Colorado from 1993 to 1997 would not have been likely to detect localized areas that fit these criteria, since the average distance between sampled points (from weight matrices) was between 219 and 264 km. The current scheme for surveying grasshopper populations is clearly inadequate for detecting the small-scale, localized infestations that contribute to eruptive grasshopper outbreaks (Lockwood and Schell 1995). The distances between survey sites must be greatly reduced to detect incipient grasshopper problems. An improved protocol would sample more sites at closer distances to increase the probability of sampling within a developing infestation. More intensive sampling would be not only more likely to meet the objective of the survey, which is to assess the potential for grasshopper densities that may require treatment on a local or county basis (USDA 1982), but also would provide better information on the location and development of outbreaks.

In summary, Colorado grasshopper densities exhibited spatial patterning at two spatial scales. Positive spatial autocorrelation was detected at scales up to 300 km. The scale of spatial pattern detected differed from year to year and with the geostatistical method used. The average distance between sampled points was an order of magnitude larger than the smallest scale at which autocorrelation was detected. These results show that while current grasshopper survey techniques are probably adequate for detecting large-scale outbreaks, localized hot-spot infestations likely will be missed. The presence of more than one scale of spatial autocorrelation in the grasshopper densities suggests that sampling for monitoring purposes should be done at frequent spatial intervals and coordinated over large geographic areas. More extensive sampling would capture the variability in abundance which reflects ecological processes operating at both the field and regional scales. The result would be an increased capacity to detect grasshopper problems, more accurate predictions of grasshopper population numbers in the next season, and increased readiness for early intervention.

Acknowledgments

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