

Dynamics in the Spatial Structure of *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae)

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ABSTRACT Integrating global positioning systems technology with a visual canopy survey, a 1-m level of sampling support was used to explore within-field spatial organization of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), in potatoes. Spatially referenced counts of adult and large larvae (third and fourth instar) *L. decemlineata* were made in four \approx 1.5-ha untreated potato fields during two Pennsylvania growing seasons. The presence and nature of spatial structure varied with developmental stage. Overwintered, immigrating adults established 'trends' or 'drift' in the mean density, but spatial dependency (covariance structure) was not detected. This, coupled with a high incidence-to-mean density relationship, suggests a within-field dispersive role for the colonizers. Large larvae and F_1 adults, in contrast, displayed spatial dependency (covariance structure), at times accounting for up to \approx 45% of the variation. Their relatively lower incidence-to-mean density relationship suggests less within-field mobility during the reproductive phase of the population cycle. These observations imply that, although an insect population's spatial structure may be difficult to characterize due to its dynamic nature, there is a consistent and predictable pattern in *L. decemlineata* spatial structure that is linked to its population phenology.

KEY WORDS global positioning systems, Colorado potato beetle, insect spatial dynamics, population dynamics, geostatistics, precision agriculture

POPULATION STUDIES OFTEN consider the spatial dimension, but what is implied by 'space' varies. In the simplest fashion 'spatial analysis' refers to mapping the geographic range of a species or population (e.g., Ali et al. 1998, Buschini 1999). Many investigators employ a spatial discussion with respect to a classification variable in analysis, such as contrasting species abundance and phenology among hosts or habitats (e.g., Bates and Weiss 1991, Boulton et al. 1992, Floyd 1996). Mathematical descriptions of spatial aggregation have historically relied on variance and mean relationships (Taylor 1961). However, though mean-variance relationships can be diagnostic of aggregation (Williams et al. 1992), this is not always the case (e.g., Young and Young 1990, Schotzko and Smith 1991). With nearest neighbor analyses, more spatial information is preserved by incorporating explicit reference to distance (e.g., Clark and Evans 1954, Dixon 1994, Weseloh 1994). Additional information, and applicability of analyses, can be gained if actual coordinates are used in the spatial analysis (Williams et al. 1992). Recently, investigators of insect populations have used a more explicit incorporation of space, formally specifying space in two-dimensional coordinates and analyzing density as a function of distance through geostatistical tools (e.g., Schotzko and O'Keeffe 1989, Rossi et al. 1992, Williams et al. 1992, Liebhold et al. 1993, Weisz et al. 1995, Sharov et al. 1996, Ellsbury et al. 1998, Tobin et al. 1999).

The Colorado potato beetle, *Leptinotarsa decemlineata* (Say), is a significant pest of solanaceous crops,

especially potatoes (Weber and Ferro 1994a). *L. decemlineata* is an invasive species of great fecundity, capable of achieving defoliating densities within a growing season (Hare 1980). With the beetle's demonstrated ability for rapid development of insecticide resistance, new strategies, such as precision integrated pest management (PIPM) (Fleischer et al. 1997, 1999, Dupont et al. 2000), are needed to aid in countering the beetle's defensive plasticity. Management experiments have demonstrated potential for significant reductions in foliar insecticide input (Weisz et al. 1996a) and insecticide resistance (Midgarden et al. 1997) with a mapped-and-targeted (e.g., PIPM) approach. To optimally implement such strategies, a better understanding of the beetle's within-field spatial organization is needed, as well as insight as to how such spatial structuring may relate to its biology and population dynamics. Relating the timing and design of sampling to population phenology, and the quality of population maps, would be improved by prior geostatistical analysis.

Sampling intensity is one constraint that has precluded more formal, explicit spatial investigation of insect density within fields. Recent technological advances in global positioning systems (GPS) permit rapid and accurate recording of field data, enhancing the feasibility of geostatistical investigations. Weisz et al. (1995) applied geostatistics to Colorado potato beetle in Pennsylvania but was limited by sampling restrictions. The present work reopens this avenue of investigation, modifying previous sampling tech-

niques to take advantage of GPS technology. The objective is to assess and evaluate within-field variation of *L. decemlineata* populations which can be attributed to spatial structuring. We used a fine scale of resolution (≈ 1 m), and describe the dynamics (change over time) of that spatial structure. Patterns found in the dynamics of these spatial characterizations are used to suggest individual and population processes driving the emergence of spatial structure in *L. decemlineata* populations.

Materials and Methods

Field Plots. Two potato ('Katahdin') fields were established during each of two field seasons near Rock Springs, PA. All fields were rotated from field corn. Fields for 1996 were ≈ 0.5 ha in size, configured as ≈ 60 by 90 -m rectangles. The area was increased for 1997 with a square configuration, ≈ 80 by 80 m (0.64 ha). Seed pieces were planted on 22–24 May 1996 and 5–7 May 1997 with 0.3 -m plant spacing and 0.91 -m furrow separation. Fields were located on a commercial farm adjacent to the Russell E. Larson Agricultural Research Center, and surrounded on all sides by field corn. Between- and within-year field locations were separated by distances >150 m but <1 km (Table 1). Each field was grided into 10 by 10 -m blocks, and marked with wire survey flags at block corners for visual orientation. The blocks encompassed 11 rows of potatoes, termed the 'block-row.'

Sampling and Data Management Protocols. We used an above-canopy visual inspection modified from Weisz et al. (1995) and Zehnder et al. (1990) to sample weekly for adults and larval instars of *L. decemlineata*. Our method varied from Weisz et al. (1995) in that two, rather than one, potato rows were scanned simultaneously by slowly walking the intervening fur-

Table 1. Distance (meters) between field centers

	1996 east	1996 west	1997 east
1996 west	942		
1997 east	157	924	
1997 west	808	268	834

row looking for beetles on the plants to either side. Additionally, a backpack GPS receiver was used to capture geographic coordinates of beetle counts. Wherever *L. decemlineata* were observed, the number of adults and each larval instar were counted within aggregations that were limited to 1 -m of row. Early in the season the fields were exhaustively sampled by surveying the entire length of every other furrow. Because of labor constraints, the number of furrows was progressively reduced as the population increased, until finally a systematic pattern was used. In 1996 a stratified random design was used for a minimum of six potato furrows, one from each block-row for each week's sampling. This stratified random design was used occasionally in 1997, but a hexagonal pattern of paired, ≈ 10 -m furrow lengths was adopted most frequently. The exhaustive design resulted in $>3,000$ and the least intensive pattern ≈ 300 1 -m samples per field.

The backpack GPS equipment consisted of an 8-channel Trimble Pathfinder ProXL receiver, a Trimble TDCI datapod (Trimble Navigation Limited, Sunnyvale, CA) and the Asset Surveyor software. Geo-referenced coordinates and associated data (beetle counts) were recorded using the datapod and then later uploaded and manipulated with the surveyor software. In 1996 we used postprocessing for differential correction to achieve 1 -m resolution (at one σ) with Trimble MCORR400 software. Base station data

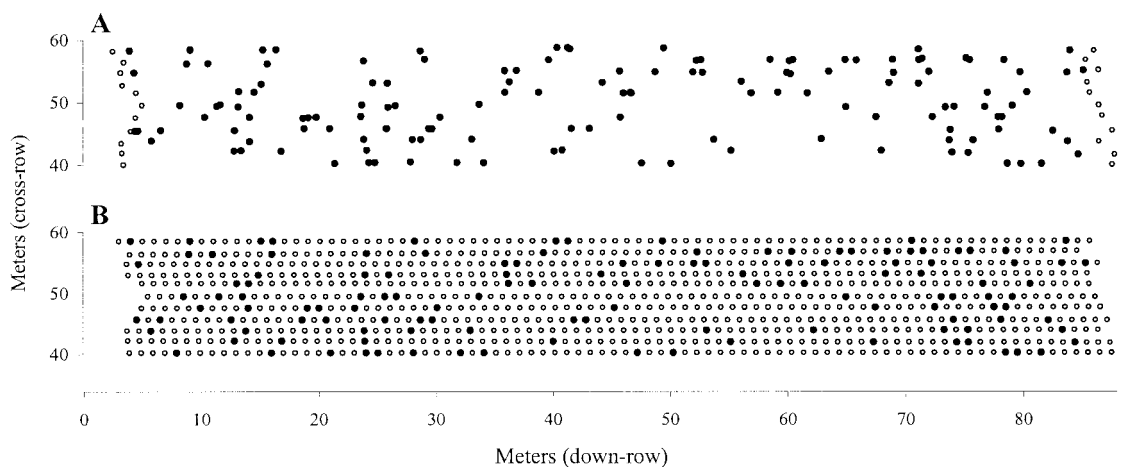


Fig. 1. An example of field data capture and processing of data for use in analyses using ≈ 20 by 80 m of the field West 1997 sampled on CD 174. (A) Posting of locations where *L. decemlineata* were observed and counted (closed circles), and the observation start and end points (open circles), along sampled transects (potato furrows). (B) Classified posting (0 and >0) of the same data after processing to construct contiguous 1 -m sampling units along the entire transect. When *L. decemlineata* location or locations occurred within a given 1 -m segment, the resulting density was posted to the segment's coordinate center (closed circles), otherwise the segment was assigned a 0 value (open circle).

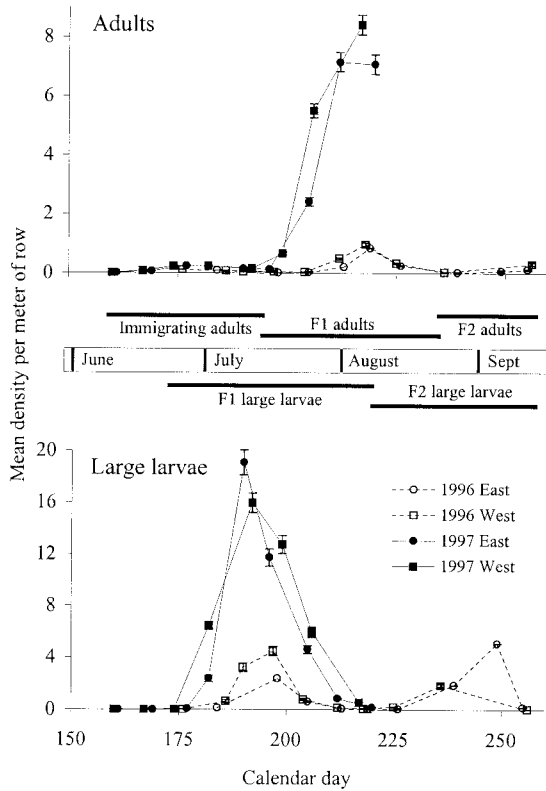


Fig. 2. Colorado potato beetle densities (\pm SE) in east and west fields during 1996 and 1997 as a function of calendar day. Vertical bars between the panels indicate beginning of the months June through September.

were downloaded from a site \approx 25 km from the research location. During 1997 a subscription for wide-area real-time differential correction was procured through OMNISTAR (Houston, TX). To optimize field time, several scouts surveyed different furrows, marking beetle locations and counts with wire-staked flags for later GPS recording. Beetle counts were scribed on the flags. Start and stop points of the surveyed furrow length were also geo-referenced for use in data manipulation (Fig. 1A). The location coordinates and corresponding count data for each observation were transferred from the TDC1 datapod to a desktop computer for manipulation and analyses.

Surveys were conducted continuously along transects, but count and coordinate data were recorded only when *L. decemlineata* were detected (Fig. 1A). Further processing was needed to represent the spatial location of *L. decemlineata* absence within the area surveyed, and to express the point-based data as density. An algorithm was constructed that took each observed transect, including its start and stop points, projected a linear regression through the x, y coordinates of the observations and end points, and then divided the transect into contiguous 1-m sample units. Observations whose coordinates fell within a sample unit were summed, expressed as density per meter,

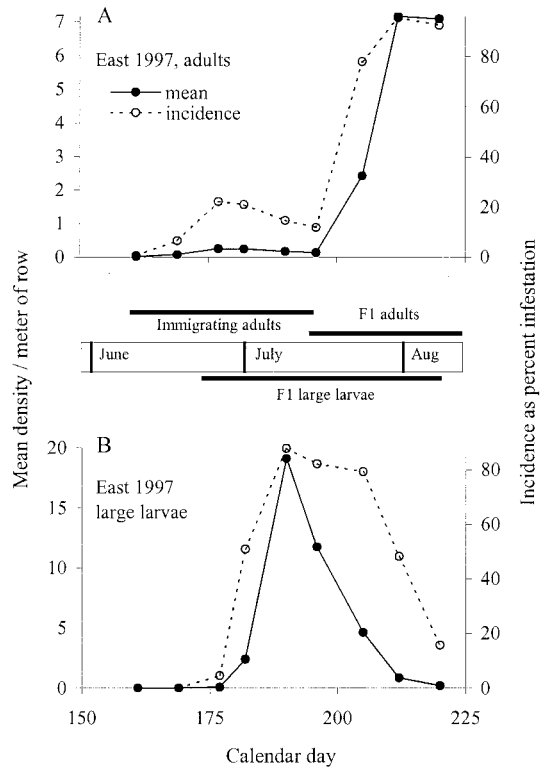


Fig. 3. Mean density (individuals per meter of row) and incidence (expressing the proportion of the field area occupied by \geq 1 individual), scaled to a proportion of the yearly maxima, of Colorado potato beetle (A) adults and (B) large larvae during 1997. Vertical bars between upper and lower panels indicate beginning of months June through September.

and posted to the center of the sample's area. A zero value was posted to the center of 1-m samples lacking any observations (Fig. 1B).

Analyses. An algorithm was constructed following Howarth and Earle's (1979) maximum likelihood approach to the generalized power transformation (Box-Cox) to determine the optimal transformation to better approximate normality. Across all data sets the best transformation was found to be \log_e , and the *L. decemlineata* density values were analyzed by field and week after transformation.

Temporal characterization consisted of field-wide mean density per week. Densities were plotted over time in two scales (degree-day [DD] and calendar day [CD]) to determine which provided the best coincidence of major phenological events across both years. Degree-day accumulation was calculated from daily minimum and maximum temperatures using a sine wave algorithm (Higley et al. 1986) with a minimum threshold of 10°C (Logan and Casagrande 1980; cf., Logan et al. 1985). Accumulation was initiated on 1 March of each year. Weather data were obtained from the meteorological station on the Russell E. Larson Agricultural Research Center at Rock Springs,

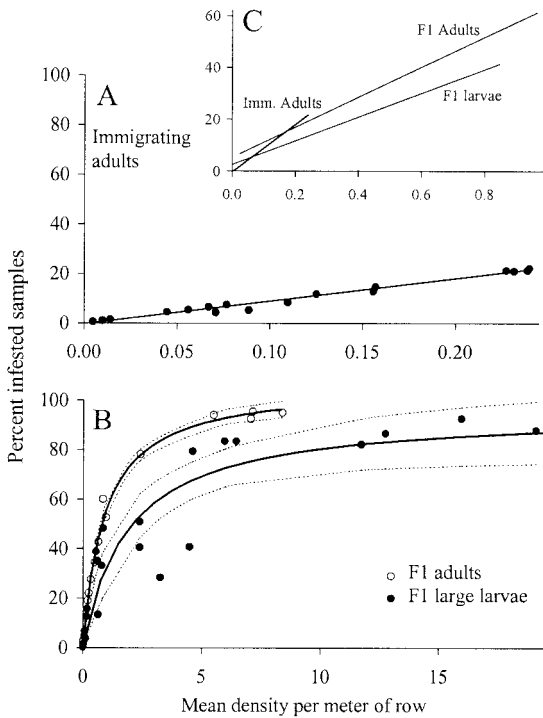


Fig. 4. Percent of infested sampling units (expressing the proportion of the field area occupied) as a function of mean density for three life stages. (A) Linear fit for immigrating adults ($N = 17$). (B) Hyperbolic model (heavy line) fit and confidence bands (dashed lines) for F_1 large larvae ($N = 23$) and F_1 adults ($N = 14$). (C) The relationship is linear for all three stages up to a density of one beetle per meter of row.

PA ($\approx 40^\circ 42' 55''$ N latitude and $77^\circ 56' 15''$ west longitude) (Stevenson and Pennypacker 1997, 1998).

Field-wide spatial trends of the mean were modeled using $z_i = \beta_0 + \beta_1 x_i + \beta_2 y_i + \beta_3 x_i^2 + \beta_4 y_i^2 + \beta_5 x_i y_i + \varepsilon_i$ (Cressie 1993) and backward elimination (SAS Institute 1989), where z_i is the density and x_i and y_i are the field spatial coordinates of the sample in meters. Regression coefficients were retained and trend models were considered significant using the SAS default of $P < 0.10$. When a significant trend was found, geostatistical analyses were performed on trend residuals, otherwise the \log_e transformed data were used (Isaaks and Srivastava 1989, Sharov et al. 1996).

Spatial dependence was examined using estimates of the correlogram function, ρ , at specified lag intervals. These estimates were made with S-PLUS S+SPATIALSTATS module (MathSoft 1997), where

$$\rho_{(h)} = \frac{\frac{1}{N(h)} \sum_{(ij):|h_{ij}=h} v_i * v_j - m_{ih} * m_{jh}}{s_{ih} * s_{jh}}$$

v_i and v_j are observation values at the head and tail, respectively, of a vector with a separating distance h . In the same way, m and s are the respective mean and standard deviations of the heads and tails of the h

separation distance. Standardized correlograms, $1 - \rho_{(h)}$, were constructed from these estimates (Isaaks and Srivastava 1989, Rossi et al. 1992). Lag separation was 1 m with a 0.5 m tolerance. Lag vectors were omnidirectional with a 22.5 degree tolerance. Spherical, exponential and gaussian models were fit to the correlograms using nonlinear regression (PROC NLIN, SAS Institute 1989) to obtain nugget and range estimates. Model selection for a given field and sampling time was chosen using the following criteria: (1) Estimating a nugget that best fit the estimates of $1 - \rho$ near the origin, (2) estimating a range closest to the correlogram's departure from the population variance, and (3) minimizing the squared residual error within the range of spatial dependence. Models were fit including lag distances out to 50 m, though lags with < 30 pairs were excluded. Those data sets showing no spatial structure were assigned the following parameter values for population comparison through time: nugget = 1, range = 0, sill = 1. Nugget estimates from the correlogram models were treated as estimates of degree of spatial dependence (cf., Williams et al. 1992) and related to dynamics (density and life stage) of the *L. decemlineata* population. We considered percent of variation that was spatially dependent to be estimated by distance between the modeled nugget and one (Isaaks and Srivastava 1989, Rossi et al. 1992).

Voucher specimens have been deposited with the Frost Entomological Museum of the Pennsylvania State University.

Results

Field-Wide Seasonal Dynamics. Although degree-day accumulation began slightly earlier in 1997, initial rate of increase was less than in 1996. Over the bulk of the growing season, cumulative degree-days for any given calendar day were greater in 1996 than 1997. Maximal cumulative degree-days in 1996 exceeded that of 1997, with the respective maxima being $\approx 1,460$ and 1,332. Population densities were plotted against degree-day accumulations and calendar days. The latter synchronized the peaks of adult immigration, F_1 large larvae and F_1 adults between years (Fig. 2), and will be used in presentation of our results.

The pattern of field means for both adult and large larvae was similar between fields within a year, but markedly different between years (Fig. 2). For adult populations, immigrating densities, which peaked in late June, were similar, but density of the F_1 adults in early August differed by almost an order of magnitude. The 1996 F_1 adults achieved a maximum density of only $0.83 (\pm 0.04)$ and $0.97 (\pm 0.54)$ per meter of row for the east and west fields, respectively, whereas F_1 adult densities of $7.15 (\pm 0.32)$ and $8.40 (\pm 0.33)$ were observed in 1997. Corresponding maximum densities for F_1 large larvae were $5.08 (\pm 0.19)$ and $4.49 (\pm 0.36)$ in 1996, whereas they were much greater in 1997 at $19.09 (\pm 0.97)$ and $15.96 (\pm 0.75)$, east and west fields, respectively. The 1996 populations went through two reproductive cycles, whereas very few eggs were produced by the F_1 generation adults of 1997, and obser-

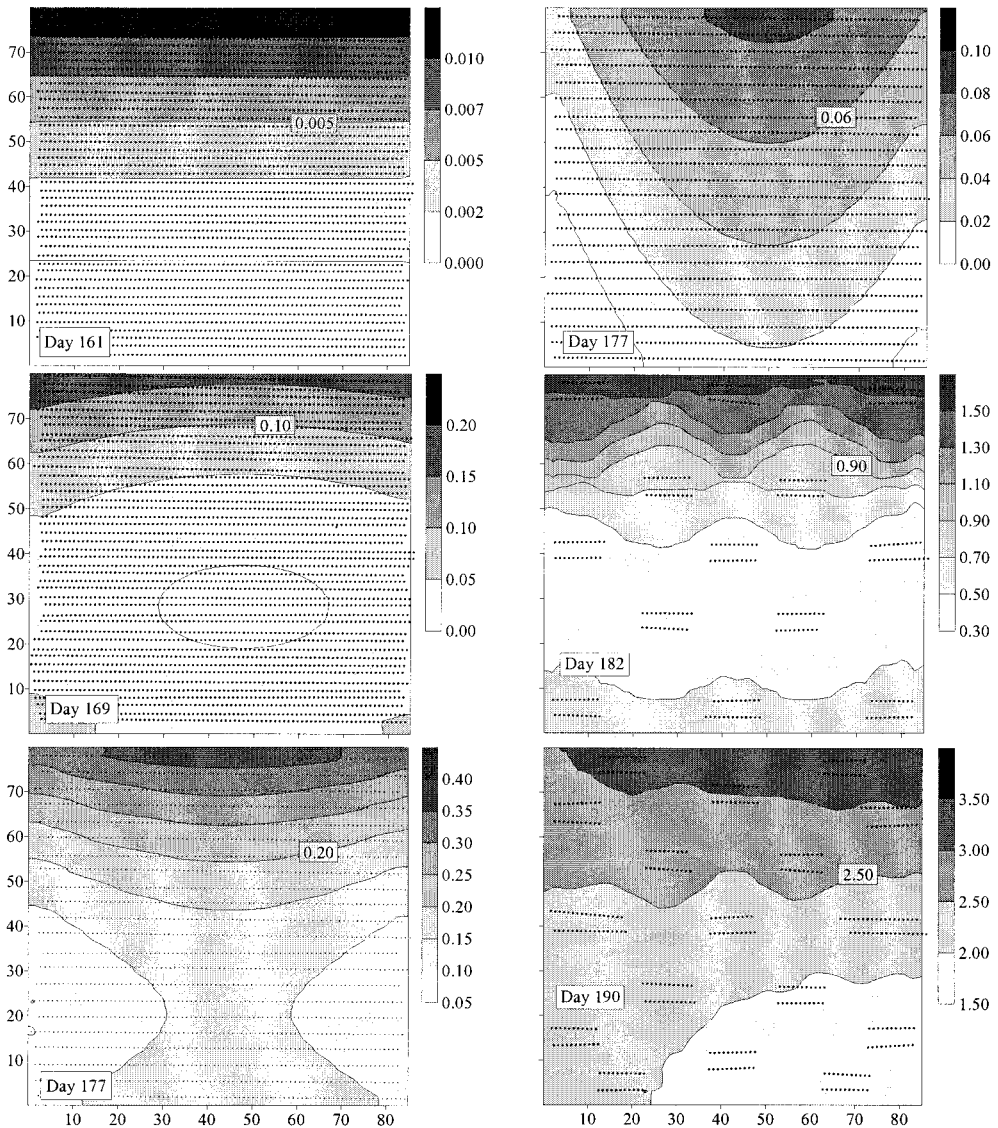


Fig. 5. Trends in the log mean density estimates (scale varies with plot) from models of adults (left column) and large larvae (right column) (field 1997 East). The large larval panel adjacent to each adult panel is from a sampling date approximately 2 wk later than the corresponding adult panel. Contour plots were constructed using a $1/d^2$ interpolation of predicted values from the trend model on a 1-m grid resolution. Dots on the contour surfaces indicate the center of the 1-m sampling units. Day equals calendar day; x and y axes are in meters.

vation of these fields was terminated after CDs 217–220 (Fig. 2). The population density during 1997 was so high that ≈ 70 – 80% of the crop was defoliated by CDs 217–220.

Movement through stages was fairly discrete (minimal overlap) during both years (Fig. 2). The peak densities for immigration occurred around CDs 176–178 (late June) for both 1996 fields, though technical difficulties had prevented capturing the onset of immigration. In 1997 the density of immigrating adults was at it highest, and nearly identical, from CDs 174 to 182 (Fig. 2). The F_1 adults peaked in early August

during both years: at CDs 218 and 219 during 1996 and CDs 212 and 220 in 1997. An emergence of F_2 adults had begun in 1996 when sampling was terminated in mid- to late September (CDs 255–256); however, the densities for these F_2 adults were very low at the last measurement. The F_1 large larvae peaked in early to mid-July in both years: at CDs 197–198 in 1996 and CDs 190–192 in 1997. There was a second peak in 1996 in September at CD 249 (Fig. 2).

Spatial Structure, Incidence. Generally, the proportion of the occupied field area (percentage of 1-m samples having one or more individuals) increased

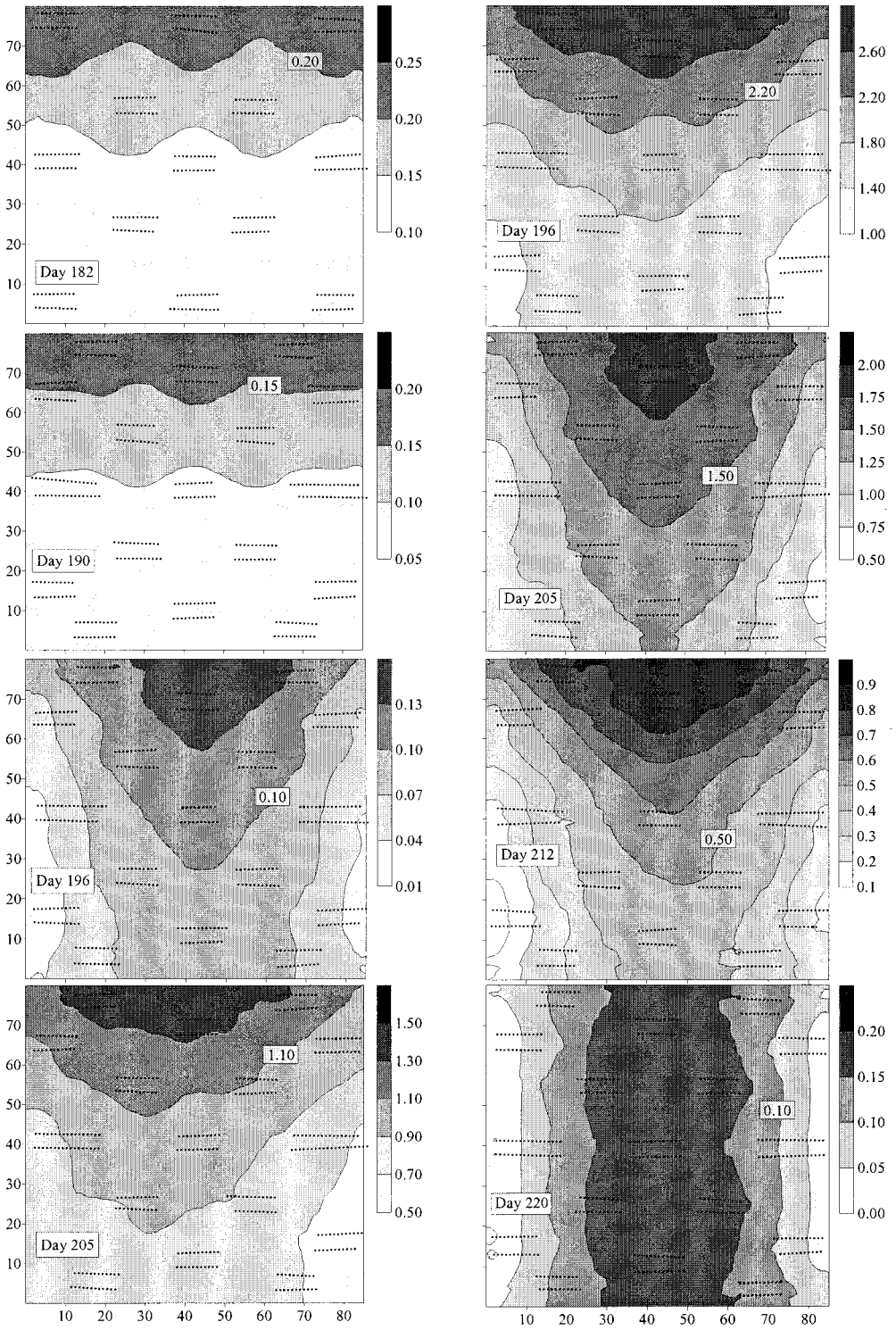


Fig. 5. Continued

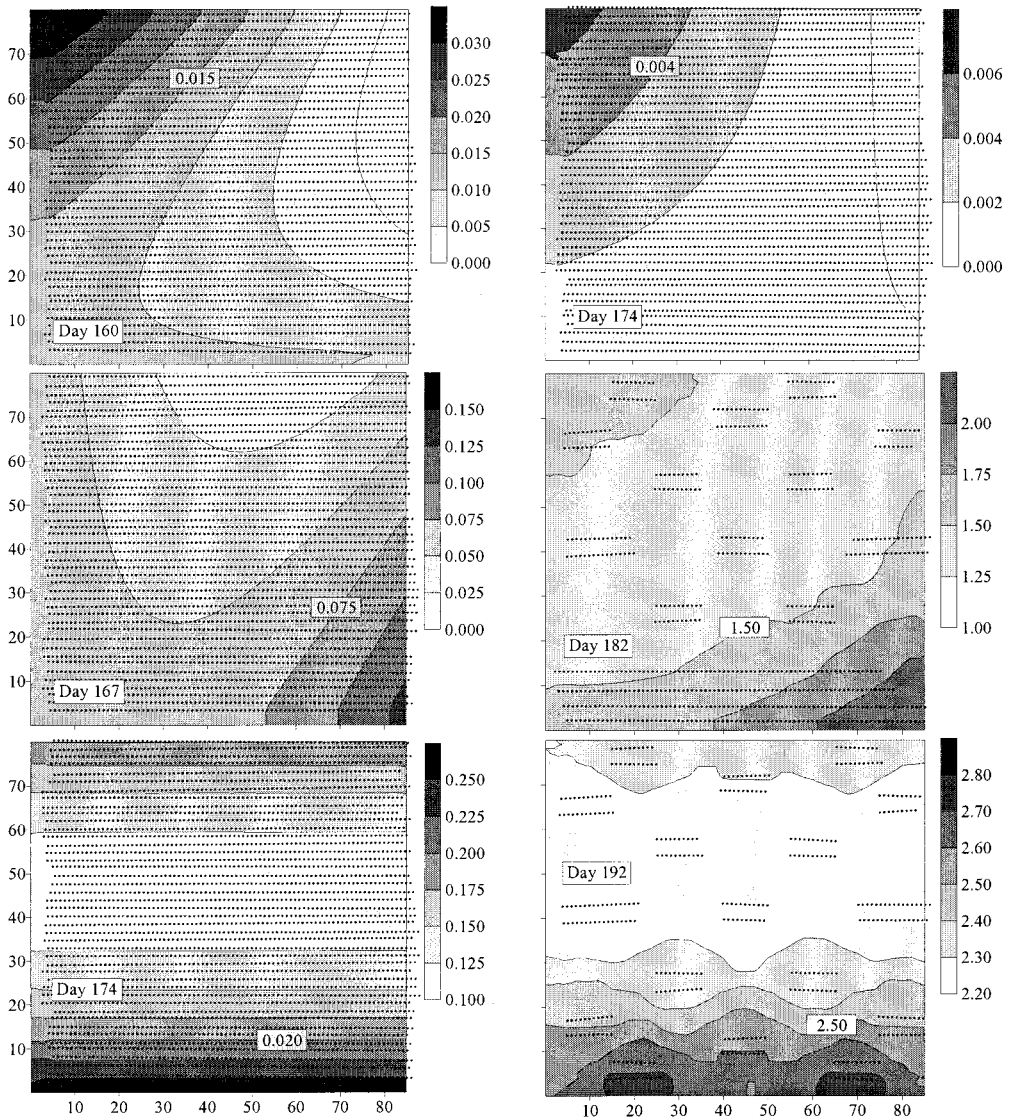


Fig. 6. Trends in the \log_e mean density estimates (scale varies with plot) from models of adults (left column) and large larvae (right column) (field 1997 West). The large larval panel adjacent to each adult panel is from a sampling date approximately 2 wk later than the corresponding adult panel. Contour plots were constructed using a $1/d^2$ interpolation of predicted values from the trend model on a 1-m grid resolution. Dots on the contour surfaces indicate the center of the 1-m sampling units. Day equals calendar day; x and y axes are in meters.

before the field-wide mean density increased, and then declined following reduction in the mean density (illustrated with field 1997 East, Fig. 3). As with mean density the magnitude of incidence was greater in 1997 than in 1996. In 1996, the large larval infestation peak varied from 55 to 81% in the west and east fields, respectively, whereas the highest infestation for this stage in 1997 was near 90%, and stayed near and above 80%, for several weeks, in both fields. Adults in 1996 increased their incidence with each generation, the greatest increase coming between immigrant and F_1 adults, but did not reach the high levels of infestation seen in 1997 ($\approx 95.0\%$).

There was a mean density-to-incidence relationship for all three life stages, but the form of the relationship differed among life stages and across the full range of densities observed. For immigrating adults in 1996 and 1997 there was a linear relationship between the mean density and incidence over the entire range of both variables [incidence = $(91.44 * \text{density}) - 0.40$] ($r^2 = 0.98$, Fig. 4A). Incidence for this stage increased ≈ 100 -fold over the corresponding increase in mean density, but immigrating adults achieved little over 20% occupation of the fields. In contrast, F_1 large larvae and subsequent F_1 adults infested up to nearly 100% of the samples. The mean-infestation relation-

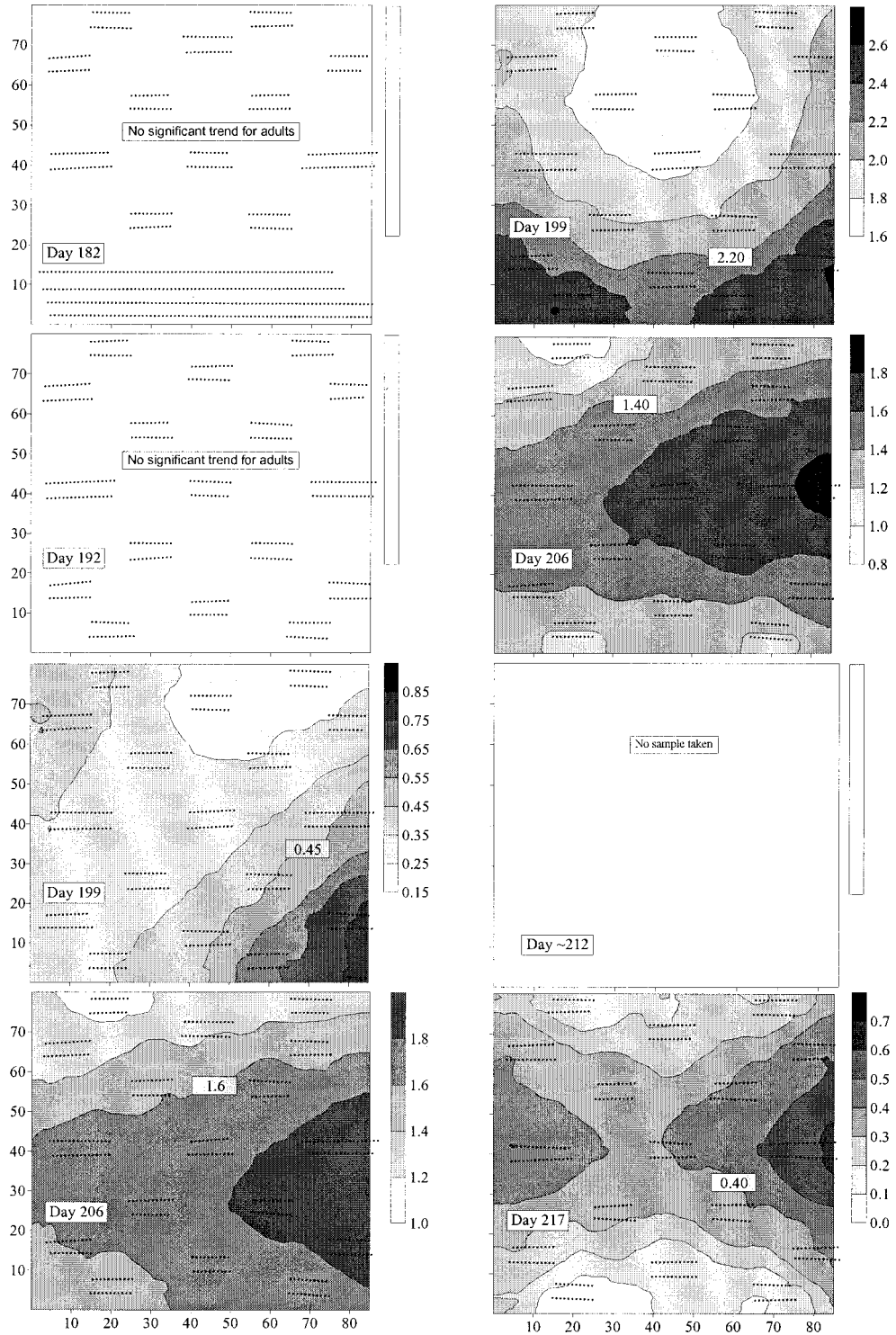


Fig. 6. Continued

ship for these latter two stages, however, was not linear and a hyperbolic saturation was fit to the relationship for both stages (F_1 large larvae, incidence =

$(95.49 * \text{mean}) / (1.91 + \text{mean})$, $r^2 = 0.86$; F_1 adults, incidence = $(106.68 * \text{mean}) / (0.90 + \text{mean})$, $r^2 = 0.99$) (Fig. 4B).

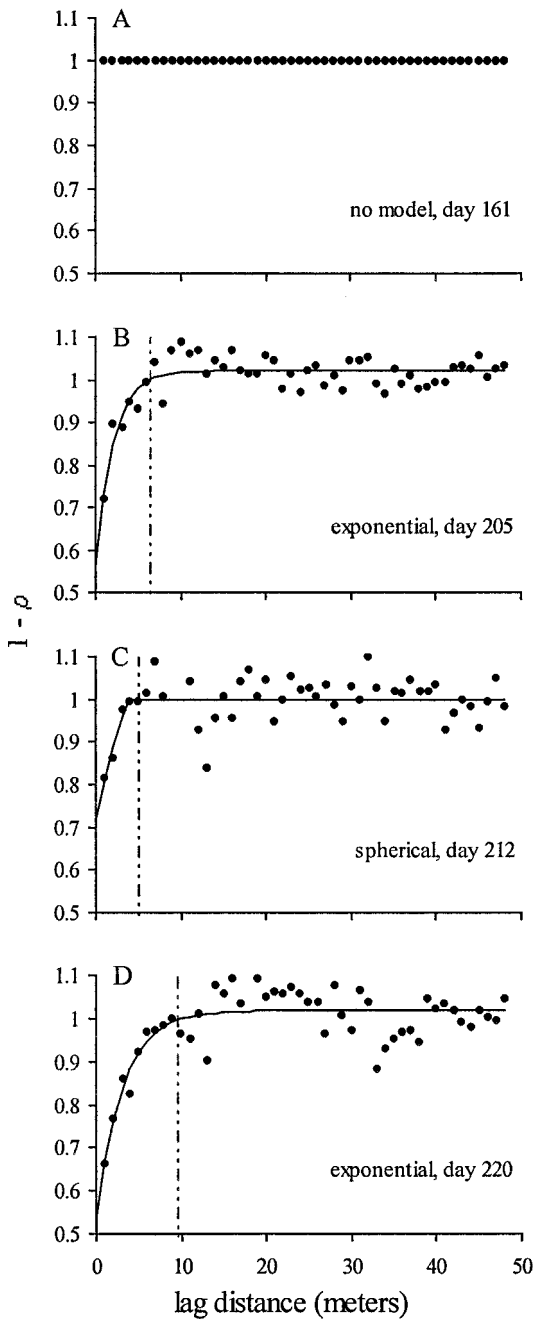


Fig. 7. Exemplary correlogram (standardized) and model fits for Colorado potato beetle adults \log_e densities or detrended residuals from East 1997. (A) Exemplifies the lack of spatial structure found with immigrating adults (CD 161). (B–D) Second-order structure found in the F_1 adults in the same field. Vertical dashed line indicates the model estimate for the range of spatial dependence.

For mean densities ≤ 1 , the relationship was linear in all three stages (Fig. 4C). Using a test for heterogeneity of slope (Littell et al. 1991), within this range

of mean density immigrating adults had a significantly greater rate of increase in incidence than the remaining two life stages ($F = 8.10$; $df = 1, 25$; $P < 0.0087$; F_1 large larvae; $F = 12.73$; $df = 1, 22$; $P < 0.0017$; F_1 adults). Within the first meter of density life stage did not significantly affect the relationship between the F_1 adults and large larvae ($F = 1.60$; $df = 1, 17$; $P < 0.2236$). When we compared these latter two F_1 stages over their entire range of densities (Fig. 4B) using heterogeneity of slope after linear transformation, we found no significant difference in the slope between the F_1 adults and large larvae ($F = 0.38$; $df = 1, 33$; $P < 0.5437$), although the intercepts were significantly different ($F = 7.62$; $df = 1, 33$; $P < 0.0094$).

Spatial Structure, Trends in the Mean Density. Trend models showed significant variation in local mean adult and large larval densities across the fields for most sampling dates. The presence and magnitude of these trends varied greatly through time. Thirty of the 36 adult data sets had significant trends ($P < 0.10$), with 19 of these significant at $P < 0.0001$. Only three of the 30 models were significant between $P < 0.05$ and 0.10 . For six of 30 models, r^2 values ranged $0.10 < r^2 \leq 0.36$, the remainder were within the interval $0 < r^2 \leq 0.10$. Characterization of the trends for large larvae was similar, with 30 of the 36 data sets having a significant trend ($P < 0.10$). Twenty-one of the 30 were significant at $P < 0.0001$, and only one was significant in the interval $P < 0.05$ – 0.10 . For 11 of 30 models, r^2 values ranged $0.10 < r^2 \leq 0.26$, the remainder were within $0 < r^2 \leq 0.10$. Estimates for the intercept ranged from 0 to $1.8 \log_e$ (density) for adults and from 0 to $3.0 \log_e$ (density) for large larvae. The remaining parameters were not great in magnitude, ranging from 0 to 0.04 for adult \log_e (density) and from 0 to 0.11 \log_e (density) in the large larvae. Exemplary interpolations of the trend models for fields with single (Fig. 5) and multiple (Fig. 6) immigration fronts are illustrated and discussed below.

Spatial Structure, Point-to-Point Dependency. In addition to across field trends, *L. decemlineata* populations displayed point-to-point spatial dependency. Inclusive of all four fields, 41 data sets from weekly observations were obtained, of which six were excluded as incomplete (weather or equipment failures). Data from the remaining 35 data sets were detrended when appropriate and then examined for spatial dependency, and correlograms indicating this second-order structure were fit with nonlinear models (Figs. 7 and 8). For the adult stage, 16 of 35 data sets indicated spatial dependency, and for the large larvae, 21 of 30 data sets showed structure beyond that explained by the trends. Of the 35 data sets for adults, 17 covered adult immigration, 14 spanned the F_1 generation, and the remaining four occurred during the F_2 adult emergence in the early fall of 1996. These last four adult data sets are not considered in most of our discussion because we were unable to observe the cohort into diapause. For the large larvae, 23 of the 30 available datasets cover the F_1 generation and seven the F_2 generation (again in 1996). As with the adults,

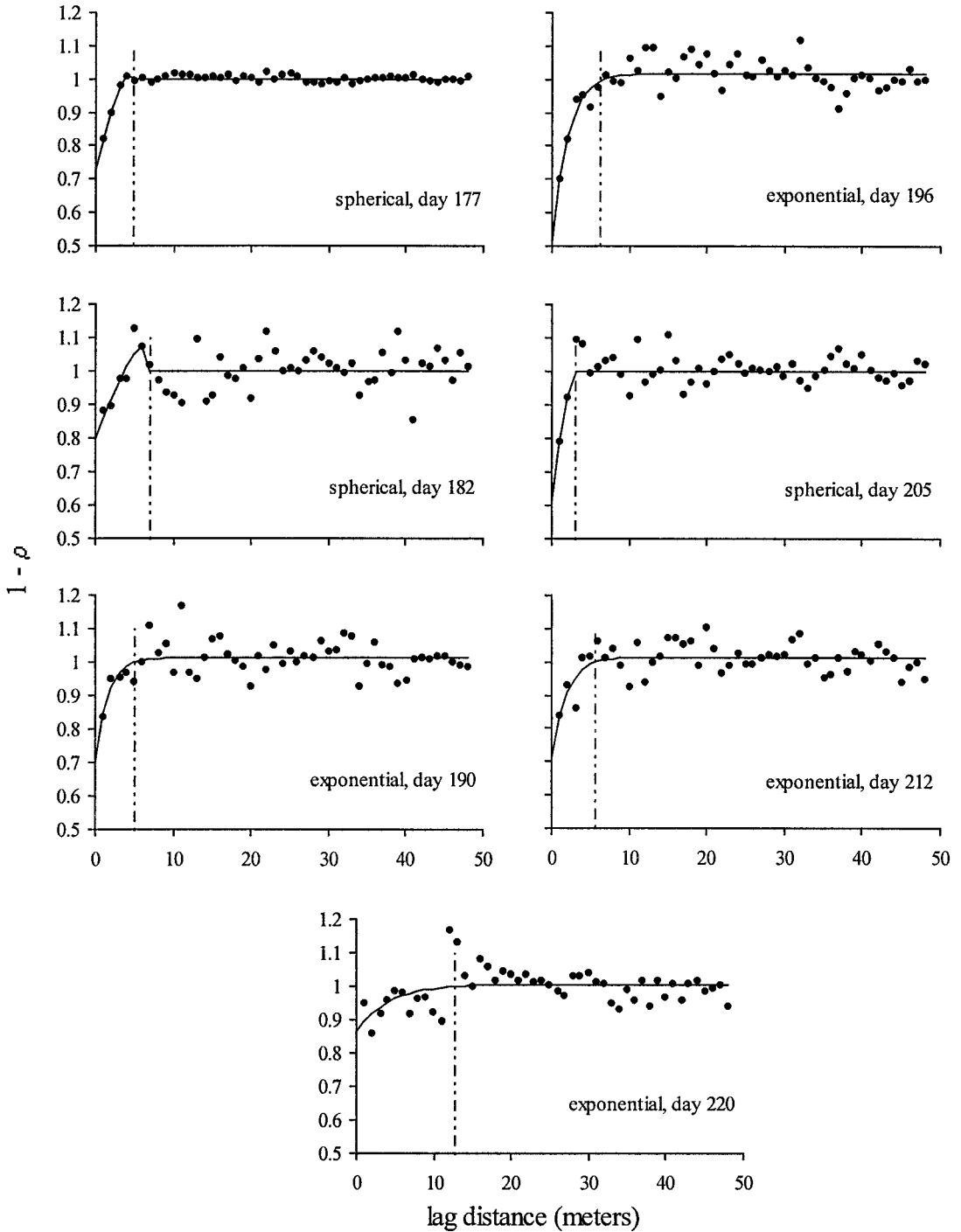


Fig. 8. Correlogram (standardized) and model fits of Colorado potato beetle large larvae \log_e densities or detrended residuals from East 1997 for all sampling dates resulting in second-order spatial structure. Vertical dashed line indicates the model estimate for the range of spatial dependence.

the F_2 large larvae data sets will not be emphasized in our discussion because these were exclusively from 1996.

The general pattern was no spatial dependency among immigrating adults (Fig. 7A), then the appearance of spatial dependency in the F_1 large larvae

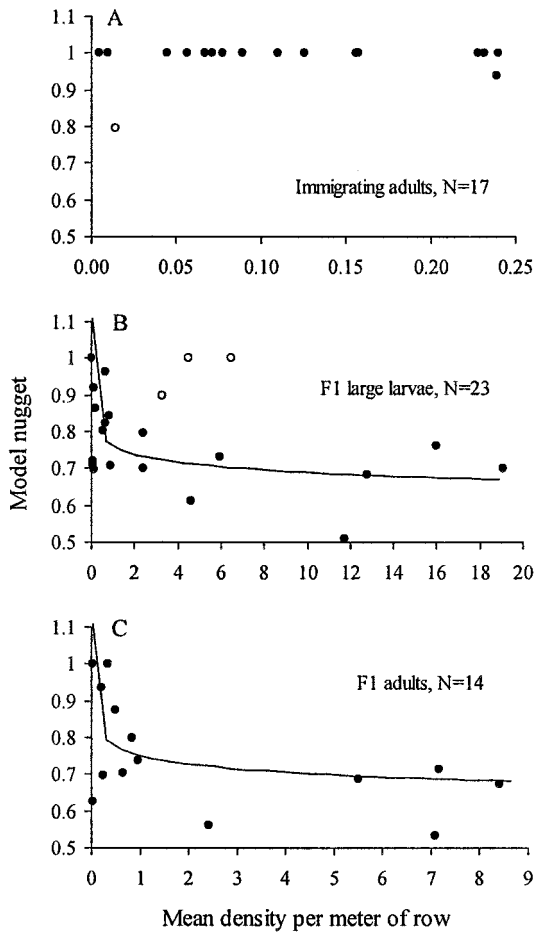


Fig. 9. The model nugget from correlograms (standardized) as a function of mean density per meter of row for three life stages. (A) immigrating adult. (B) F_1 large larvae. (C) F_1 adults. Nonlinear fits are included to illustrate the relationship. Open circles are data points not included in the model fit for the large larvae.

(Fig. 8), with the persistence of this structure into the F_1 adults (Fig. 7 B–D). To examine the dynamics of this structure, the nugget was plotted as a function of population density (Fig. 9). In 16 of 17 instances immigrating adults showed no spatial structure (nugget estimates ≈ 1 , Fig. 9A) across the entire range of densities. For the F_1 large larvae there was a decreasing nugget (increasing spatial dependency) with increasing density. The nugget decreased in an exponential pattern with density for 20 of the 23 estimations (Fig. 9B, solid circles, nugget = $0.82 * e^{\text{density} * -0.015}$, $r^2 = 0.25$). This correlation with density continued for all 14 nugget estimations in the F_1 adults (Fig. 9C, nugget = $0.81 * e^{\text{density} * -0.018}$, $r^2 = 0.51$). Thus, the percent variability explained spatially, that is, the difference between the model nugget ($1 - \rho$) and 1 (no correlation), ranged from 0 to 20 for immigrating adults, 0 to 49 for large larvae, and 0 to 47 for F_1 adults.

Considering only data sets resulting in spatial dependency, estimates for the range of spatial depen-

dence varied from 0 to 16 m (15 of 16 instances being < 10 m) and 0 to 24 m (19 of 21 instances being < 10 m) for adults and large larvae, respectively. The range of spatial dependence varied greatly, but did not display a consistent relationship with density as in the nugget.

Discussion

Field-Wide Seasonal Dynamics. Though between-year planting date and weather varied greatly, the timing of stage-specific density peaks corresponded better between years on a calendar day than on a cumulative degree-day scale. Given the importance of temperature for an insect's metabolic rate, we had expected cumulative degree-days to provide the best scale in synchronizing between-year *L. decemlineata* population dynamics. The somewhat unexpected asynchrony may be explained by the importance of other cues (e.g., photoperiod) for triggering population synchronizing events (e.g., possibly overwintered emergence, time of host plant emergence, immigration, mating, oviposition) in *L. decemlineata* dynamics. Timing of plant emergence is likely to be important in this situation, because first observation of potato emergence was made from CD 153 to 159 over both years, even though planting date differed by ≈ 17 d. A scale such as calendar day, which is highly correlated with thermal accumulations but also incorporates other factors (such as photoperiod), is likely to better synchronize the population dynamics of *L. decemlineata* between years.

Spatial Structure, Incidence. Incidence, or the percentage of samples having one or more beetles, is one measure of the proportion of a field occupied when samples are collected throughout the field. Comparing the pattern of mean density against incidence may be useful for understanding spatial structure in a population or particular life stage. The more rapid increase of incidence compared with mean density during adult *L. decemlineata* immigration (Figs. 3 and 4 A and C) suggests that these individuals are spatially active within the field, and are not only responsible for immigration to the field, but are also the principal agents for within-field dispersion. Further evidence for high activity of the immigrants is that, despite their sparse population at any given observation, the adults must have moved extensively throughout the fields because the F_1 large larvae occupied up to 95% of the sample locations. Weber and Ferro (1994b) found movement of marked, overwintered adults within a potato field of up to ≈ 20 m from their release point, which is consistent with our anecdotal observations of within-field flight events. Such high individual activity, constrained within a relatively short spatial radius, could certainly result in the high incidence of later large larvae and F_1 adults, while preserving the spatial trends and the near lack of covariance spatial structure of the immigrating stage.

Interpretation of the mean density-to-incidence relationship is different for the F_1 large larvae. Although they are capable of moving up to 75 m when resources

are exhausted (Cass 1957), large larvae are likely to have high spatial fidelity, with their particular location a result of oviposition and survivorship. The hyperbolic relationship of mean density-to-incidence for this stage (Fig. 4B) is likely shaped by two phenomena. First, infestation increases a week (or two) before the mean achieves corresponding proportions, then, after the population has peaked, the mean declines more rapidly than percent infestation (e.g., Fig. 3). These dynamic periods are both reflected in the steepest part of the mean density-to-incidence curve, which occurs at lower densities (Fig. 4B, $\leq 60\%$ infestation occurring below mean densities of five *L. decemlineata* per meter, with most points below two *L. decemlineata* per meter). During the early part of the development of this stage the mean density-to-incidence relationship would suggest a widespread (i.e., in many to most sampling units) recruitment of precocious individuals into the stage. That is, a time of high incidence to low or moderate mean density. The same relationship of high incidence to lower mean density occurs after population density peaks (Fig. 3B, CD ≈ 190 –210), with individuals late in recruitment to the stage also being late in progressing out of the stage (either to the next stage or dying). Thus, the steep part of the mean density-to-incidence relationship (Fig. 4) is influenced by the temporal distribution of cohort recruitment and loss. The asymptotic part of the relationship reflects the time surrounding the peak of the large larval period. Early recruits have entered the stage in nearly all of the sampling locations across the field and so incidence is at its maximum. The remaining individuals enter the stage, eventually increasing density to the maximum.

Given the overall fidelity of non-emigrating F_1 adults to their location of emergence (Alyokhin and Ferro 1999), both the extremely high incidence of F_1 adults corresponding to that observed in the F_1 large larvae (Fig. 3) and the similar shape of their mean density-to-incidence relationship can be expected (Fig. 4B). The explanation for this relationship is likely the same as that for the F_1 large larvae, with the curve smoothing somewhat by minimal movement of these adults expanding the incidence slightly earlier in development of mean density.

The difference in the mean density-to-incidence relationships between immigrating adults and subsequent F_1 stages (Fig. 4) reflects the greater within-field movement by immigrating adults. Comparison of the relationship over the 0–1 beetle/m range shows a linear fit in all three stages. However, the slope of the immigrant's plot is significantly greater than that of the F_1 stages, indicating greater rates of occupation of the field by the overwintered adults.

Spatial Structure, Trends in the Mean Density. Immigration had an important role in establishing and shaping *L. decemlineata* within-field trends. This was most obvious in the 1997 East field (Fig. 5). The northern edge of this field was oriented toward the 1996 East field location. Weisz et al. (1996b) modeled risk of infestation as a declining function from a previous year's potato crop, and found that risk increased sig-

nificantly if the locations were separated by < 1 km. The east fields of 1996 and 1997 were separated by only 157 m (center-to-center) (Table 1), and immigration was heavy along the northern border of the 1997 East field (Fig. 5, left column). The first immigrants arrived around CD 161 and their presence, principally along the north field perimeter, developed a steep trend declining rapidly across the field. Subsequent immigrants (though in less number) were found along the southern perimeter also, and the adult population was increasing toward the field center. This established a gradient in the mean density, which was maintained throughout the summer for both adult (Fig. 5, left column) and larval stages (Fig. 5, right column), with the larval populations lagging behind adults ≈ 2 wk.

Patterns become more complex with multiple fronts of immigration. The 1997 West field received *L. decemlineata* pressure from two different directions. Immigrating adults began arriving around CD 160 in the NW corner of the field. Sampling the following week detected another front coming from the south, initially concentrated on the SE corner. The southern immigration, while arriving slightly behind that from the NW, was of greater intensity and rapidly dominated within-field population spatial dynamics. As with 1997 East, these immigration fronts can be attributed to the location of potato fields in the previous year. One field (not in this study) was 177 m (field center-to-center) to the NW and the 1996 West field was 268 m to the SSW. Being significantly closer, the former field is likely responsible for the early colonization of the NW corner. Although beetles from 1996 West took longer to find the field, its large population rapidly dominated, shaping the trend from the south. The 1996 East field, which was 808 m to the east, may have also contributed some immigrants. A fourth field from 1996 (again not in this study) 843 m ENE of 1997 West may also have been a small contributor to the 1997 West population.

By CD 174 the 1997 West field adult population was near maximum density and the trend had established high areas along the northern and southern edges, declining toward the field center (Fig. 6, left column). Sampling from the subsequent 2 wk found no significant trends associated with the adults. A possible explanation is that the mean density across the field equalized as the population developed inward along both invasion fronts and established in the field center. Patterns for the large larvae mirrored that of the adults with an approximate 2-wk lag during the first 3 wk of development (Fig. 6, right column). The following week (CD 199), as the larval population begins to decline, the trend inverts. This new, inverted pattern is maintained through CD 217, and is likely the result of progressive transition to the pupal stage, beginning first in the areas of earliest colonization and highest density, then working inward toward the center of the field.

Although immigration appeared to drive much of the within-field trends it was apparent that defoliation played a role for the F_1 adult population. With the emergence of F_1 adults around CD 199, one can see a

trend reminiscent of that established during immigration (Fig. 6). However, by CD 206 and 217 the trend was highest in the middle of the field and toward the east. Although the shape of this trend is similar to that of the larval population as it transitioned to pupation, it more likely represents within-field relocation by the emerging adults. Alyokhin and Ferro (1999) reported little within-field movement by nonemigrating F_1 adults. However, their observations were under conditions less stressful than those experienced in our 1997 West field. Without control measures the *L. decemlineata* population defoliated most of the potatoes in areas where the densities had been the highest. The shift in trend by the emerging adults represents their movement to areas of the field where plants retained greater foliage.

Trends for 1996 fields (not displayed) are more difficult to compare with immigration because locations for the previous year's *L. decemlineata* populations were unknown and the GPS technology was not implemented until after adult immigration had begun, especially in 1996 East. Field 1996 West developed a population along its eastern border and NE corner that could be consistent with a single source for immigrants. Correspondingly, trends over time in this field developed for both adults and large larvae either distinctly east to west or NE to SW across the field. As with 1997, the trend was dynamic having the greater mean estimates moving toward the center as the population developed across the field through time. Missing data early in this season made it impossible to interpret adult immigration trends in field 1996 East, but trends subsequent to this suggest two or more fronts of immigration.

Spatial Structure, Point-to-Point Dependency. We hypothesized that if spatial dependence was going to be present, at some point in the recruitment of individuals to the population (or a given life stage) spatial dependency will become evident, rise to a maximal level, and then decay, finally disappearing with population senescence. Our observations were consistent with this hypothesis, with two components, stage phenology and density, influencing the spatial dynamics. The significance of stage phenology was evident, as seen by transition from immigrants to F_1 , whereas correlation with density was evident within F_1 life stages. An implicit assumption is that sampling error was random among fields and dates. An increase in sampling error at low densities could result in an increased nugget effect. We sampled at a fine resolution with a large sample size to minimize this error. We believe that any increase in sampling error associated with low densities was minimal because many of these values occurred early in the season when we were able to census or nearly census the fields (resulting in a higher n) and the crop canopy was small.

The near lack of spatial dependency in the immigrating adults is not surprising considering their colonizing function and generally low densities. The relatively high within-field activity patterns discussed above would counter tendencies toward aggregation. Thus, immigrating adults contributed to spatial dy-

namics by establishing trends in local means within fields, but point-to-point spatial aggregation was not detected. Had spatial dependency (aggregation) been observed with this stage, we might hypothesize it to be a function of mating behavior or host plant quality, either for consumption or oviposition.

Although the majority of observed trends (mean structure) were established by adult immigration, consistent spatial dependence (covariance structure) appears with the first generation of large larvae. Like the trends, point-to-point spatial dependence was dynamic in these large larval and F_1 adult populations. This dependency structure was maintained or slightly enhanced during the subsequent adult emergence (F_1). This is not to say the F_1 large larvae are responsible for establishing the spatial dependency. The second-order structure may be a relic of adult oviposition preferences or spatial heterogeneity in egg, first or second instar survival.

Using density, incidence, and phenological stage to follow the life course of these *L. decemlineata* populations we found spatial dependency in large larvae and F_1 adults to follow the progression of all three. Because incidence correlated well with density (Figs. 3 and 4), both had a correspondingly similar relationship to spatial dependency (Fig. 9), although incidence was not as distinct (not figured). The nature of the mean density-to-dependency relationship was similar between the large larvae and F_1 adults (Fig. 9) as observed with the mean density-to-incidence relationship described above (Fig. 4). However, though this exponential decrease in dependency mirrors the shape of incidence over similar density values, each relationship offers different biological information. Whereas incidence is concerned with the presence or absence of individuals in each isolated sample unit, spatial dependency relies on the *number* of individuals *between* sampling points. Thus, the F_1 populations, which were well established throughout the field (indicated by the incidence relationship), were also truly aggregated (spatial dependency). These aggregations were not sharply circumscribed as the percentage of variation explained by the spatial dependency asymptotes at ≈ 30 – 40% in both large larvae and F_1 adults (Fig. 9). This dependency structure was reached rapidly however, being achieved with densities less than or equal to two *L. decemlineata* per meter.

We cannot, from these data, infer that spatial dependency is caused by density. Even though there is a strong relationship between mean density and the nugget, we did not manipulate density with respect to other plausible driving forces; i.e., *L. decemlineata* developmental stage. The relatively steep exponential decrease in the mean density-to-dependency curves (Fig. 9) suggests that there may be a threshold for the detection of second-order spatial structure. Obviously, one cannot have structure without individuals, and the density-nugget relationship may indicate that the population must achieve a certain magnitude before spatial dependency can be characterized (with a given level of support; here 1 m).

The range in spatial dependency Weisz et al. (1995) found for *L. decemlineata* was ≈ 65 m. Our results differed, suggesting a range ≈ 10 – 15 m at the most. Several things may account for this disparity. First, is field scale, with Weisz et al. (1995) using fields slightly larger than ours. They also had dramatically different sample units. Although our samples are based on point observations converted to 1-m (approximately square) segments of potato row, their samples were based on a full 13.7 m of linear row. Finally, and probably most influential, is that Weisz et al. (1995) did not detrend their data before geostatistical analysis. Detrending before computation of variograms (or correlograms) is important as a field-wide trend can obscure or misrepresent spatial dependence. If an investigator desires experimentation with a process reflected in the covariance spatial structure, independent samples (of transformed residuals) can be established with separation distances >15 m. For mapping the *L. decemlineata* population, both the within-field trend in local means and point-to-point covariance structure in F_1 populations should be considered (Isaaks and Srivastava 1989).

By using density and categorizing the *L. decemlineata* population into phenological stages we were able to characterize explicit spatial structure and its dynamic nature. Spatially the immigrating adults in their colonizing role serve as the within-field dispersers (supported in mean density-to-incidence relationships) and establish the initial and principal trends in mean density relative to the direction of overwintering locations. Thus, landscape position relative to overwintering reservoirs (especially last year's solanaceous fields) influence spatial patterns of immigrant adults which determine the principal trend structure. But there is little to no spatial structuring at a 1-m sampling scale beyond this trend. This is very different than the spatial structure of subsequent stages, which bear the population's reproductive role. The large larvae and F_1 adults we observed maintained the generalized trend structure established by the immigrant population, with the caveat that F_1 adults established an alternate trend structure in the face of extensive defoliation at high densities. While spatial dependency was not found with the immigrants, aggregate structure beyond trends could be detected in the established within-field population. Within these two stages the structure was dynamic, developing with increasing density.

Several factors may contribute to the transition from lack of spatial dependency of immigrants to the structure found with the F_1 generation. Females may be spatially selective about oviposition sites, perhaps driven by host plant quality or microclimate differences which are spatially structured. Differential survival of eggs or the first two larval instars could also have given rise to the patterns we observed. Again, this structuring in survival may be imposed via microclimatic or host quality, or through spatial patterns displayed by predators or parasitoids. Examining for structure at finer resolutions of life stage (egg masses, small larvae), and explicitly measuring spatial struc-

ture of putative processes (e.g., stage-specific survivorship rates) may promote development of spatially explicit population models.

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