

Modeling Colonization of Overwintered Immigrant *Leptinotarsa decemlineata* (Coleoptera: Chrysomelidae)

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ABSTRACT Colonization of potato (*Solanum tuberosum* [L.]) fields by Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae), has often been recognized as a process that initially results in an edge-biased spatial pattern. We modeled this spatial process by measuring distance of immigration for individual overwintered adults. Distance was measured to the nearest field edge or to the field edge along a radial vector from the field center. The frequency of beetles captured within 1-m distance intervals was modeled as an exponential decay function of distance from the edge for both measurement methods. Expression of the results as a cumulative frequency has management implications for spatial deployment of control measures against immigrating beetles and applicability for spatially explicit simulation of the within-field population dynamics of the beetle. Managers might use such models to estimate the proportion of immigrating adults that would be affected by border treatments of a plant systemic or transgenic insecticide as a function of the width of the treatment.

KEY WORDS *Leptinotarsa decemlineata*, CO potato beetle, colonization, immigration, mapping

THE COLORADO POTATO BEETLE, *Leptinotarsa decemlineata* (Say), is a pre-eminent pest on solanaceous crops worldwide, and much research has focused on different components of its variable population dynamics (Weber and Ferro 1994a). One such focus has been host location and immigration of this specialist pest to host fields. As with many aspects of *L. decemlineata* biology, overwintered immigrating adults display a broad range of behavior. Under conditions of intense cultivation, with rotated or nonrotated fields in close proximity, the beetle appears to invade by walking from adjacent hedgerows (French et al. 1993). In contrast, where distances are greater, flight seems to be an additional important immigration mechanism (Ferro et al. 1999). With either scenario, the tendency is for the greatest beetle densities to develop around the field perimeter (Weisz et al. 1996a), and thus, perimeter tactics have been suggested for management (French et al. 1993). Blom et al. (2002) found a perimeter application of imidacloprid (a systemic insecticide) of ≈ 5.5 m greatly reduced the within-field

population of *L. decemlineata*. This resulted in an increase in yield greater than expected given the area treated. However, yields in the perimeter treatment were still significantly lower than those of the whole-field treatment of imidacloprid, and the distribution of potato sizes in the perimeter-treated fields did not differ from untreated fields. They suggested that additional spatial information about the immigration pattern of *L. decemlineata* could greatly improve the effectiveness of a border treatment targeted at overwintered immigrating adults.

L. decemlineata has been the subject of many simulation-modeling investigations. Simulation has been used to model temporal dynamics of *L. decemlineata* population means, phenology, and development of resistance (Konovalov and Malinina 1979, Kurth et al. 1986, Ewing et al. 1994, Follett et al. 1995, Arpaia et al. 1998). These models, however, have not incorporated spatially explicit parameters. The spatial patterns of *L. decemlineata* populations have been described as a dynamic series of trend models, with a covariance structure developing for later life stages (Blom and Fleischer 2001). The trends in the local mean density were generally predictive of patterns measured in later larval life stage in untreated fields (Blom and Fleischer 2001, Weisz et al. 1996a). Thus, an improved understanding of initial *L. decemlineata* immigration could be a key component to understanding spatial patterns of later life stages. The objective of the current study was to characterize the explicit spatial pattern of postdiapause *L. decemlineata* adult immigration.

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Materials and Methods

A single 0.80-ha field of potatoes (cultivar 'Katahdin') $\approx 80 \times 100$ m was planted during the growing seasons of 1999 and 2000 on or adjacent to the Russell E. Larson Agricultural Research Center (Rock Springs, Centre County, PA). Potato rows were spaced at ≈ 0.9 m, and the within-row interplant distance was ≈ 0.3 m. Fields were rectangular with their centers located at 40.72273°N latitude and 77.92012°W longitude and 40.72165°N latitude and 77.93788°W longitude in 1999 and 2000, respectively. The fields were not planted in solanaceous crops during the previous year. In 1999, the field was ≈ 1.5 km from 1998 potato fields. In 2000, the field was within ≈ 200 m of 1999 potato and tomato fields. Each morning, beginning at ~ 0730 h, the fields were surveyed exhaustively for previously unseen (new) adult immigrants (those not marked during a previous survey, described below). The daily survey was usually completed within 2–3 h and consisted of slowly walking each furrow, visually searching for adult beetles in the canopy to either side.

The location of each new adult was flagged, and the elytra of the beetle was marked with nail polish for future recognition (Boiteau 1986, Williams 1988). A variety of methods have been used for marking adult *L. decemlineata* (Caprio et al. 1990, Weber and Ferro 1994b), including that by Unruh and Chauvin (1993), who developed an elytral puncture method for unique marking of up to 16 million individual beetles. While elytral punctures may be the definitive method for identification, practical limitations imposed by our study (speed and distant visibility of the mark) led us to prefer the use of a small amount of bright fingernail polish placed on the elytra.

After the survey, the geographic coordinate for each new immigrant (flagged position) was determined using a backpack GPS receiver (Trimble XRS) and datapod (Trimble TDC-1). GPS location estimates were corrected real time in 1999 using the OMNISTAR service, and with postprocessing in 2000 using the Pennsylvania State Land Analysis Lab base station located ≈ 10.5 km from the field. Surveys were conducted from the time plants were first emerging until adult immigration had ended. Developmental degree-days were calculated from daily minimum and maximum temperatures using a sine wave algorithm (Higley et al. 1986) and a base threshold of 10°C (Lashomb et al. 1984, Logan and Casagrande 1980, cf. Logan et al. 1985). Accumulation was initiated on 1 March of each year. Weather data were obtained from the KPSU Automated Surface Observing System (Rock Springs, PA), $\approx 40^\circ 43.24'$ N latitude and $77^\circ 55.90'$ W longitude (≈ 0.5 and 1.0 km from the 1999 and 2000 fields, respectively).

We made some simplifying assumptions because we were unable to determine the vector, mode (flight versus walking), or time of entry for each immigrating beetle. First, we assumed that initial observation of the position of a beetle within a 24-h period would be representative of its location at entry (Bach 1982, cf.

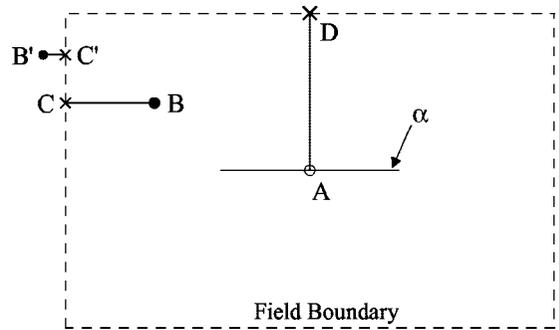


Fig. 1. Schematic of the perpendicular method used to calculate the distance between the position of each beetle (B) and the nearest field edge (C). This distance (BC) was also expressed as a proportion of the maximum possible perpendicular distance (BC/AD), which in a perfectly square field would be the shortest distance from the field center (A) to any field boundary (e.g., D). In a rectangular or trapezoidal configuration, the maximum perpendicular distance from opposing edges meets along a line (α) rather than at the field center (A). Two sides of the potato fields had a ragged boundary resulting from the unequal start and stop in planting of the potato rows. This meant some beetle positions (B') fell outside of the average boundary established for computations along row-end edges of the field. For these positions, the distance to edge was computed as (B'C') and the proportionate expression as (B'C'/AD).

Blom and Fleischer 2001). Thus, even if this is not the exact plant location of entry for the beetle, it represents the spatial tendency of the individual during the early stages of colonization. A second assumption was that each beetle enters the field either: 1) along a path perpendicular to the field edge nearest its point of initial discovery (Fig. 1), or 2) on a trajectory toward the field center (Fig. 2). If we assume a perpendicular entry, then the distance of each beetle into the field can be expressed in absolute terms (meters) or as a proportion of the maximum possible perpendicular penetration (Fig. 1). If we assume a radial trajectory,

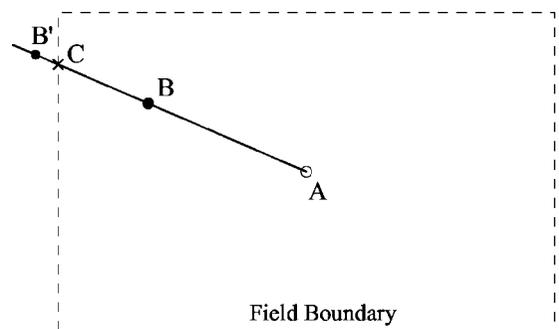


Fig. 2. Schematic for the radial method used to estimate the distance of each beetle from the field edge (BC) along a bearing defined by a line from the field center to the position of the beetle (AB). This was also expressed as a proportion of the entire distance from field center to boundary (BC/AC). When beetle positions (B') fell outside of the average boundary, the distance to edge was computed as (B'C) and the proportionate expression as (B'C/AC).

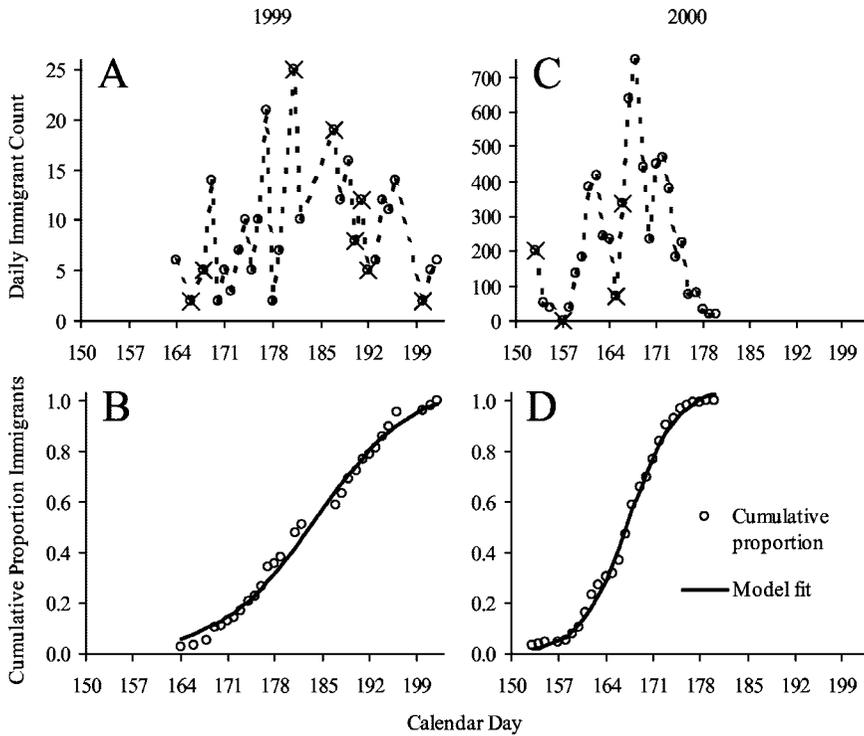


Fig. 3. Time course of overwintered *L. decemlineata* immigration. Upper panels (A and C) trace the daily counts for each year with circles crossed out to indicate surveys excluded from distance analyses. Lower panels express the immigration as a cumulative proportion of the total immigrants. Both years were fit with a logistic function (B and D) (Table 1).

then a vector can be established from the point at which the path of the beetle would intersect the field boundary and the field center (Fig. 2). Each relationship of the beetle to the field edge could then be characterized by the distance into the field (Fig. 2, line BC) and as a proportion of the entire vector (Fig. 2, BC/AC). These are rather generous assumptions, although it seems they would be robust within a management context: a relationship between beetle frequency and distance from field boundary could be used directly for applying perimeter plant systemics or transgenic insecticides. The relationship developed along a radial vector, as opposed to a perpendicular vector, would be more amenable for populating fields with *L. decemlineata* under computer spatial simulation.

Field boundaries used for distance-from-edge calculations were established from four field corners. There were some irregularities to the start and stop locations of the row ends, creating a ragged edge of potatoes at two ends of the field. The boundary corners were adjusted to minimize capturing nonplanted space within the field boundary and the orphaning of potatoes outside the boundary. Thus, we considered the row-end field boundaries an approximation or average boundary. Inevitably, a few beetles landed on these orphaned plants, and because we could not exclude them from the data set (they were responding to their perceived edge of the field), our best approximation of their distance relationship was to calculate

their perpendicular departure from the average field boundary as B'C' (Fig. 1) and proportion of maximal perpendicular distance as B'C'/AD (Fig. 1). The radial calculations for these individuals were handled in a similar fashion, with B'C as the departure from edge and B'C/AC as the proportion (Fig. 2). Although this was not a perfect solution, it seemed more preferable than using negative distance values for beetles recruited to the fields, or fixing outside beetles to the boundary, which excessively and erroneously created zero distance values.

Data Analysis. Previously, we observed that calendar day works better than degree-days for comparing major population events of *L. decemlineata* between years in this geographic area (Blom and Fleischer 2001). Given this observation and the fact that these data are calendar based, calendar day has been preferred in model development. Degree days have been referenced for comparison with the *L. decemlineata* literature. All beetle observations were used in this time course characterization. Cumulative daily proportion of total immigrants was modeled as a logistic function of day of immigration equation: $y_t = K / (1 + [-re^{(t-t_{50})}])$, where y_t = cumulative proportion of immigrants at time t , K = the asymptote, maximum immigration, r = proportional rate of immigration, t_{50} = time to 50% of K , and t = time (d), the day of immigration beginning with observation of the first immigrant.

To characterize the spatial process, frequency of the distance of beetles from the nearest edge was calculated for 1-m intervals (bins). Only individual locations that were known to have occurred within the previous 24 h were used in these analyses. If a daily survey was preceded by a missed day of observation or one that had been incomplete (e.g., rained out), the locations were not used in the distance analyses. The data were best fit to an exponential decay function: $y_d = Ae^{(rd)}$, where y_d = number of or proportion of total immigrants in distance bin d , A = estimate of intercept or frequency of immigrants at field boundary, r = rate of decline in immigrant frequency, and d = distance from field boundary (1-m wide bin). All parameters for equations 1 and 2 were estimated using the nonlinear regression procedure of the SAS software (SAS 1989, PROC NLIN).

One could hypothesize that the frequency of immigrant beetles is a function of the absolute distance into a field. Alternatively, the relationship may vary with spatial scale, or be a mixture of these two extremes. Therefore, relationships for beetle frequency were developed as a function of the distance from the field edge in meters and as a function of the proportion of the maximum possible distance from the intersecting field edge. These latter models were developed to permit future testing of the relationship at different field scales. Finally, to permit generalizing these relationships to different levels of immigration pressure, the frequency values were modeled as a proportion of the maximum immigrants detected against both absolute and proportionate distance from the field boundary.

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

Results

The 1999 field was located ≈ 1.5 km from *L. decemlineata* research plots of the previous year and, as a result, received little pressure from overwintered adults ($N = 262$, immigrants). The immigration also began later than usual, with the first adult sighted on 14 June. We surveyed through 22 July (39 calendar days, ≈ 402 degree days) (Fig. 3A). Of the 262 beetles observed, 184 were available for distance analyses (Fig. 4A). In contrast, the 2000 potato field was within ≈ 200 m of potato and tomato fields from the previous year. Over the course of 28 d (2–29 July, ≈ 263 DD), we observed immigration of 6,342 overwintered adults (Fig. 3C), of which 5,730 were available for distance analyses (Fig. 4B). Thus, 78 or 29.8% and 612 or 9.6% of the immigrants were excluded from analyses for 1999 and 2000, respectively. Of those beetles included, only a few had landed outside the average boundary. In 1999, coordinates for only one beetle were 0.13 m beyond the north boundary. Of the 5,730 beetles in 2000, 130 (2.3%) were outside the boundary for an average distance of 0.55 m (SE = 0.035). The majority of these (112, 2.0%) were within 1 m of the boundary (mean = 0.43, SE = 0.024), with only 17 (0.3%) in the

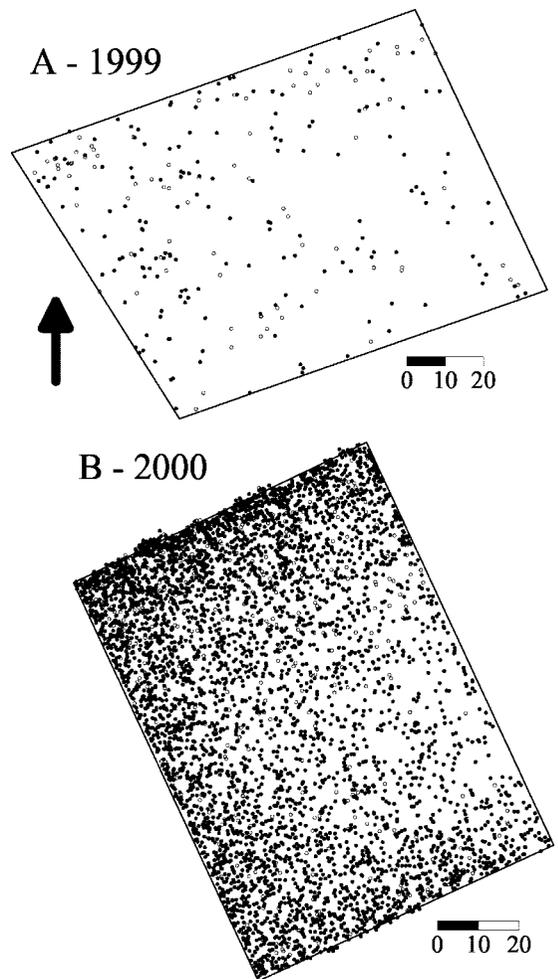


Fig. 4. Within-field location of first sightings of individual overwintered adult *L. decemlineata* in 1999 (A) and 2000 (B). Closed circles indicate locations used in the distance analyses, while open circles indicate locations that were not used, as the time interval from the previous field survey was >24 h. Arrow indicates north. Potato rows were in the east-west direction during 1999 and north-south in 2000. The line surrounding each field indicates extents used for calculation of distance to field edge for each beetle coordinate.

1- to 2-m interval. Only one beetle was positioned beyond this at 2.35 m outside the boundary.

Logistic fit (equation 1 to the immigration time course (Fig. 3, B and D)) was significant for both years (1999, $F = 2971.58$; $df = 3, 26$; $Pr > F < 0.0001$; 2000, $F = 6581.02$; $df = 3, 24$; $Pr > F < 0.0001$). Estimation of the asymptote was similar between years, although the other parameters differed (Table 1). The rate of increase nearly doubled in 2000 over 1999, and the duration of immigration was shortened by ≈ 4.5 d in 2000. Correlation among the parameters was minimal, except between r and t_{50} during 1999. Residuals indicated reasonable fit for the models.

Models of exponential decay (equation 2 fit data relating immigrant adults and distance from field

Table 1. Logistic models fitting the cumulative proportion of total immigrants to the day of immigration (initiated with observation of first immigrant)

Year	Parameter	Estimate	Asymptotic SE
1999	<i>K</i>	1.07	0.035
	<i>r</i>	0.14	0.008
	<i>t</i> ₅₀	21.07	0.684
2000	<i>K</i>	1.05	1.051
	<i>r</i>	0.29	0.286
	<i>t</i> ₅₀	16.41	16.409

1999, *N* = 262, 2000, *N* = 6,342.

boundary during both years (Fig. 5)). These relationships were modeled with combinations of the distance and frequencies being expressed using their actual values and as proportions of the respective maxima (Table 2). All models were significant (*F* tests, *P* < 0.0001), and values for asymptotic correlation indicated little redundancy in the parameters. Residuals were reasonable in both magnitude and pattern.

Similar, but slightly different parameter values were estimated between distance methods (perpendicular or radial) within year (Table 2). The number or proportion of adults at the field edge, which is estimated by the *y*-intercept (parameter *A*), was greater using the perpendicular method (e.g., 529.5 versus 460.3). When actual distances were used, the rate of decline in immigrant frequency from the field edge (*r*) was generally steeper with the radial method (e.g., -0.04

versus -0.05), although when distance was scaled to the method maximum, the perpendicular method had the greater rate value (e.g., -1.92 versus -2.19).

The 1999 models for distance, using both the distance methods, were closer to a linear relationship than in 2000 (Fig. 5). In 1999, there was a spike of high frequency centered at 20 m from the field edge, but this was not observed in 2000. The accumulated predictions of the proportion of total immigrants estimated from the exponential decay models are shown as a relationship to distance from field boundary for both the perpendicular (Fig. 6, A and B) and radial (Fig. 6, C and D) methods. By accumulating predictions from exponential decay models, we estimate that ≈80% of the *L. decemlineata* immigrant within ≈18–25 m of the field boundary using perpendicular computations, or ≈23 and 30 m using radial calculations (Fig. 6).

Discussion

These data support the observations that the *L. decemlineata* immigrates to and has greater population development near field edges (French et al. 1993, Weisz et al. 1996a, Blom and Fleischer 2001). Managers could use the relationships like those shown in Fig. 6 to estimate the border width of a plant systemic or transgenic insecticide needed to achieve a desired mortality of immigrant adults.

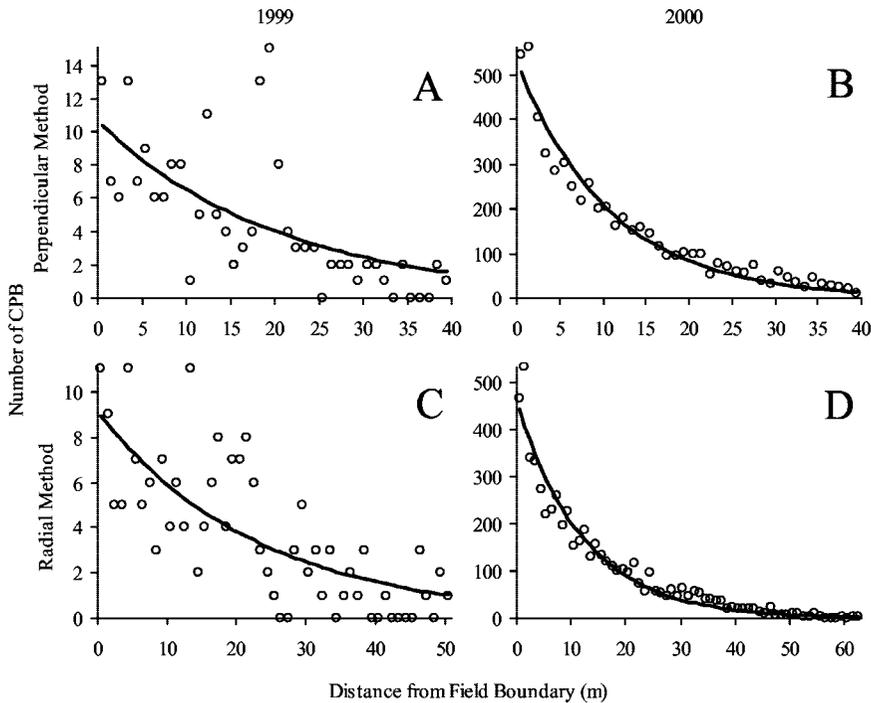


Fig. 5. Frequency of overwintered *L. decemlineata* immigration as a function of distance from the nearest field edge in 1999 (*N* = 184) and 2000 (*N* = 5730). (A and B) Perpendicular distances to the nearest boundary; (C and D) nearest distance to field boundary measured along a vector from the field center. The axes are scaled to their respective maxima so that the model fits represent the shape expected when counts are expressed as a proportion of the total (Table 2).

Table 2. Frequency or proportion of adult *L. decemlineata* immigrants (CPB) modeled as an exponential decay with distance from the field boundary

Year	CPB	Distance Scaling	Parameter	Estimate	Asymptotic SE	
Perpendicular Method 1999	Frequency	Meters	A	10.61	1.466	
			r	-0.05	0.011	
		Proportion	A	10.61	1.466	
	Proportion	Meters	r	-1.92	0.430	
			A	0.06	0.008	
		Proportion	A	0.06	0.008	
2000	Frequency	Meters	A	529.50	17.546	
			r	-0.09	0.004	
		Proportion	A	529.50	17.546	
	Proportion	Meters	r	-3.66	0.173	
			A	0.09	0.003	
		Proportion	A	0.09	0.003	
Radial Method 1999	Frequency	Meters	A	9.13	0.924	
			r	-0.04	0.007	
		Proportion	A	9.13	0.924	
			r	-2.19	0.345	
		Proportion	Meters	A	0.05	0.005
				r	-0.04	0.007
	2000	Frequency	Meters	A	460.30	14.255
				r	-0.08	0.004
			Proportion	A	460.30	14.255
		Proportion	Meters	r	-5.13	0.225
				A	0.08	0.002
			Proportion	A	0.08	0.002
			r	-5.13	0.225	

Distance was represented in either meters or as a proportion of the maximum. 1999, $N = 184$; 2000, $N = 5,730$.

The perpendicular method of computing the shortest distance to boundary is the simpler, and accumulated predictions from its decay model are better suited for informing management decisions when a border tactic is planned. Under these circumstances, prediction of beetle coordinates is not needed, nor would the border estimate depend on the biological accuracy of the methodological assumption (perpendicular entry to the field). The concept of a border itself is equivalent to the perpendicular approach, being defined by shortest distance to edge. Modeling the frequency decay as a function of distance from edge allows conditioning of a border treatment to fit particular situations or management needs (border width = X percentage of cumulative frequency). Given reasonable predictions of immigration pressure (perhaps developed from Weisz et al. 1996b) and the population size a given field can withstand, a manager could specify the percentage of immigrants to be killed, then use the cumulative predicted frequency-to-distance relationship (e.g., Fig. 6, A and B) to implement an appropriate width of a perimeter tactic. In a similar fashion, the relationship could be used in a resistance management program: knowing the necessary number or proportion of the population required to maintain adequate susceptibility, width of the pe-

rimeter tactic could be adjusted to encourage the needed survivorship.

Assumptions behind the radial method of computation are an attempt to achieve greater biological realism. We made the assumption that if the beetles are originating from any appreciable distance, the field will be a point (larger or smaller depending on distance) within the landscape. Thus, the location of a field in the immigration path between a beetle and field was represented by the geographic center of the field. By using a vector based on the center of the field, the closest distance to edge and the distance to the border along the vector are by definition no longer synonymous. As a consequence, distances to edge computed with the radial method will be inherently greater than those under the nearest edge, perpendicular framework (see Fig. 6). Thus, if applied to management, the radial method would certainly be more conservative than the perpendicular. It would follow that this method, and its added realism, may be preferred when a directionally biased immigration is anticipated and one wants to incorporate consideration of the subsequent within-field trends (Blom and Fleischer 2001).

This investigation does not address the effects of field scale. Our observations are limited to a field size

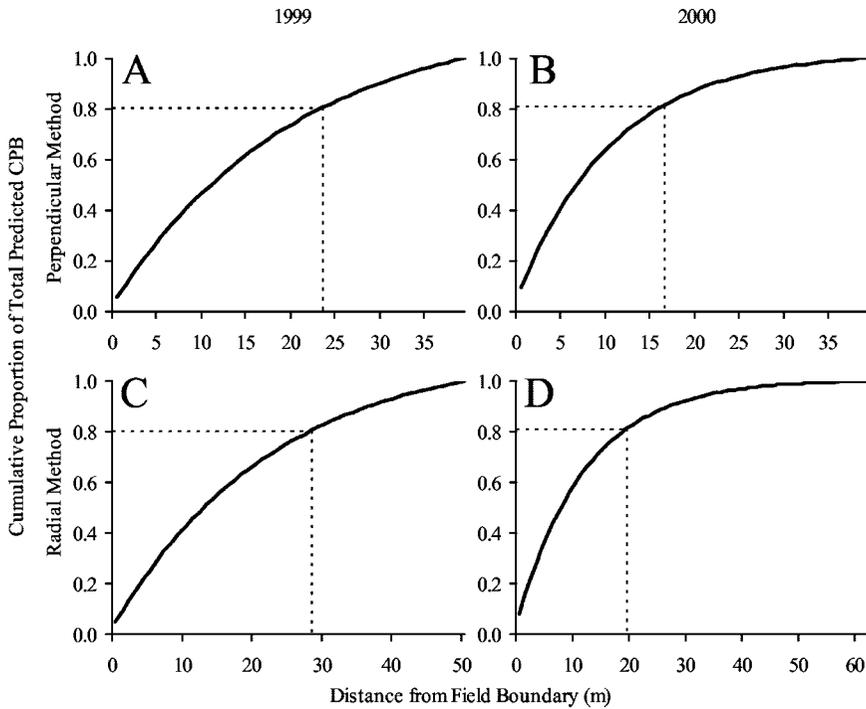


Fig. 6. Cumulative exponential curves of immigrating overwintered *L. decemlineata* derived from exponential decay predictions (equation 2) for 1999 and 2000 using either the perpendicular or radial method for establishing the distance from the field boundary. Each panel has been scaled to represent the proportion of the total *L. decemlineata* immigrants predicted. Dashed lines indicate distance from field boundary within which $\approx 80\%$ of total immigrants are expected.

of $\approx 80 \times 100$ m. To compensate somewhat for this limitation, we have modeled the frequency-distance relationship as a proportion of the maximum possible immigration distance in addition to modeling with the actual distance values. The relationship expressed in actual distance may prove stable over increasing field size or, conversely, it may be extremely sensitive to field scale. If the former situation prevails, exploitation of the relationship would be simple for pest management. We anticipate the relationship to behave somewhere between these two extremes.

Regional scale may also prove important to the within-field frequency-distance relationship. Over the first 20 m of distance from the field edge, the probability of immigration in 1999 was consistently less than in 2000 (Fig. 6). Of course, the relationship in 1999 is based on a much smaller number of individuals than experienced in 2000, which is consistent with the effects of increasing distance between overwintering site and potato field (Weisz et al. 1996b, Follett et al. 1996). Increasing distance delays the onset of immigration and attenuates the period of immigration (Fig. 3; Lashomb and Ng 1984, Lashomb et al. 1984, Weisz et al. 1994). We followed immigration for 39 calendar days (≈ 402 DD) in 1999, while immigration ended in 28 calendar days (≈ 263 DD) during 2000. Further investigation is needed to refine the colonization spatial profile across various scales.

This between-year difference in distance from overwintering sites could have affected the mode of

colonization, and thus distance of establishment in toward the field center (influencing model parameters, Fig. 5; Table 2). One could hypothesize that a large number of the beetles reaching the 2000 field may have done so by walking, and thus established themselves on plants nearer the border. Conversely, beetles in 1999 may have arrived mostly through flight, and thus, a greater proportion might have reached further in toward the center of the field.

Although further work is warranted on the influence of both field and regional scales, this investigation contributes both a method and initial results toward development of a spatially explicit model of the colonization process. It also provides a quantitative framework for relating border-management tactics to this process.

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