Dispersal and Spatiotemporal Dynamics of Asian Longhorned Beetle (Coleoptera: Cerambycidae) in China

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ABSTRACT We studied dispersal and spatiotemporal dynamics of the Asian longhorned beetle, *Anoplophora glabripennis* Motschulsky, in Gansu Province of north central China. We used mass mark–recapture methods and observed that 98% of beetles were recaptured within 920 m from a release point, whereas the median dispersal rate for all recaptured adults was 30 m/d. Dispersal potential within the course of a season for males and gravid females was 2,394 and 2,644 m, respectively; however, more work is needed to evaluate the potential of long-distance dispersal events to initiate new colonies outside current U.S. quarantine boundary guidelines. We observed that tree size and number of existing emergence holes on a tree were significant positive predictors of new emergence holes, but we did not measure a significant effect of tree size, number of existing emergence holes, and number of new emergence holes on adult beetle abundance. Implications of these findings within the context of host quality are discussed, but more research is needed to identify key factors in the multiyear host colonization process. Peak population abundance of unmarked beetles (i.e., background populations) in both 1999 and 2000 occurred between 800 and 900 degree-days (base threshold = 10°C) from 1 January. Background populations exhibited local spatial autocorrelation during peak abundance, with ranges of spatial dependence of 229–543 m. The implications of this study are discussed in reference to the role that *A. glabripennis* population biology plays in the current eradication effort.

KEY WORDS *Anoplophora glabripennis*, invasive species, mark–recapture, spatial autocorrelation, eradication

THE ASIAN LONGHORN BEETLE, *Anoplophora glabripennis* Motschulsky, native to China and Korea, was initially discovered infesting trees in the United States in 1996 (Haack et al. 1997). Infestations have been reported in Chicago, IL, New York City, and Long Island, NY, and most recently in Jersey City, NJ. The beetles attack a variety of host trees, including maple (*Acer* spp.), elm (*Ulmus* spp.), willow (*Salix* spp.), and poplar (*Populus* spp.), and larvae are particularly damaging to the cambium and xylem in which they feed. Nowak et al. (2001) presented a worst-case scenario of the inimical effects of *A. glabripennis* establishment in several U.S. urban landscapes, with potential losses exceeding $600 billion.

Because of these risks posed by *A. glabripennis*, coupled with the fact that current known infestations are thought to be limited in scale, efforts to combat this beetle are focused on eradication. Currently, individual trees are inspected visually to detect *A. glabripennis*. However, this survey method is both labor- and time-intensive, and its efficacy is questionable. Once trees are found to be infested, they are removed and quarantine boundaries are established around the source point. The Animal Plant Health Inspection Service (APHIS) current guidelines call for eradication surveys to extend one-half mile from the infested location. Because these surveys are the most expensive component of the eradication effort, their optimization would represent a major benefit to the Asian Longhorn Beetle Eradication Program, both in terms of cost saving and increased detection efficiency. Studies of dispersal and spatial dynamics would improve our understanding of the population biology of *A. glabripennis* and consequently would facilitate the development of optimal sampling procedures.

The modeling of insect dispersal has received considerable treatment from both a theoretical and applied perspective (Southwood 1978, Okubo 1980, Rudd and Gandor 1985, Corbett and Plant 1993). The dispersal behavior of *A. glabripennis* has been studied previously. Wen et al. (1998) used mark–recapture experiments in the Ningxia region of northern China. They observed that the average beetle dispersed 106 m from a release point, whereas a few marked adults were recaptured from the farthest sampling location, which was 280 m from the release point. We previ-

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Table 1. Tree composition of the study area by transect vector

Direction	No. of hosts			No. of nonhosts[a]	% of host trees	% of poplars among hosts
	Poplar	Willow	Elm			
East	1,359	137	29	695	68.7	89.1
Southeast	1,492	97	50	872	65.3	91.0
South	1,503	164	43	1,353	55.8	87.9
Southwest	2,167	115	118	2,143	52.8	90.3
West	835	208	98	1,180	49.2	73.2
Northwest	842	140	113	1,091	50.1	76.9
North	1,038	195	33	1,056	54.5	82.0
Northeast	1,144	121	85	1,727	43.9	84.7
				Mean (±SD)	55.0 (8.3)	84.4 (6.6)

[a] Includes (among others) pepper (*Capsicum* spp.), tree of Heaven (*Ailanthus altissima* (Miller) Swingle, apple (*Malus* spp.), and *Paulownia* spp.

ously reported from the Gansu Province of north central China, by using similar methods, mean dispersal of 266 m (Smith et al. 2001). As with the study reported by Wen et al. (1998), we also recaptured some marked beetles from the most outlying sampling locations, which were 600 m from the release point. Indeed, the recent infestation in New Jersey motivates the question of the possibility of *A. glabripennis* to disperse longer distances, because the closest known infestation to New Jersey was >1.6 km and separated by the Hudson River. We thus extended our sampling boundaries and reinvestigated movement by *A. glabripennis* adults.

The estimation of spatial autocorrelation is a useful ecological tool for recognizing spatial variation at both large and small scales (Cressie 1993). Its theoretical basis is that the autocorrelation between pairs of sample values can be described as a function of distance and direction in a spatial vector. If two data that are close to each other in space and are more similar in value than two data farther apart, then the variable is considered to be spatially autocorrelated (Matheron 1963, Isaaks and Srivastava 1989, Rossi et al. 1992, Liebhold et al. 1993). Spatial autocorrelation estimates can be used to determine the required sampling scale to obtain spatially independent samples. Furthermore, sampled values can be used in interpolating algorithms to predict abundance at unsampled locations in space (Isaaks and Srivastava 1989, Fleischer et al. 1999). There is little known information regarding the spatial dynamics of *A. glabripennis.* In this article, we studied dispersal of *A. glabripennis* in China by using mark–recapture methods. We also studied the spatial and temporal distribution of the background population by modeling phenology and estimating spatial autocorrelation.

Materials and Methods

Dispersal. We conducted our study ≈1 km west of Liu Hua, which borders the Yellow River in Gansu Province of north central China. We used *A. glabripennis* adults that were of known age (newly emerged) and of unknown age. The former were collected from tree bolts (≈1.5 m in length) of *Populus nigra* L. variety *thevestina* (Dode) Bean, which were amassed ≈50 km from the study site. Bolts were transported to the center of study site and placed under a cage. As adults emerged from these bolts, they were marked and released. The latter were collected from outside the study site, transported to the center of the site, and marked and released on the same day that they were collected. Unique coloration of the pronotum allowed differentiation of beetles of unknown and known ages, as well as differentiation of beetles released on different days.

Known- and unknown-aged beetles were released from a center point of the study site. Transects radiated from this center in eight directions: north, north east, east, south east, south, south west, west, and northwest. Both unmarked and marked individuals were counted at sampling points along each transect. Sampling points ranged from 100 to 1,080 m from the release point and were located at ≈100-m intervals, depending on tree locations and landscape characteristics. Each sampling point consisted of a group of *P. nigra* trees that were sampled weekly from 1 June to 30 September 2000. From 1 June to 11 August, these groups consisted of 6–28 trees, and the median (interquartile range, IQR) number of sampled trees per group was 18 (15–20) ($n = 1430$ trees). To increase the probability of recapturing marked adults, we added 1,320 trees among all distances and directions from 18 August to 30 September, resulting in a median (IQR) number of sampled trees of 28 (19–46) per group during this period.

A census of all trees (sampled and unsampled) along the transects was conducted to gather information on tree species composition (Table 1). We sought to select a study site such that the effects of variation in host composition were minimized across transects as much as the landscape permitted. Across all transects, an average of 55% of the trees were known *A. glabripennis* hosts, specifically those in the genera *Populus, Salix,* and *Ulmus;* among hosts, ≈84% were poplars (Table 1). Although host compositions did differ among transects, a correspondence analysis (PROC CORRESP, SAS Institute 1999) revealed that due in part to the dominance of poplars irrespective of vector, ≈71% of the variation was due to differences in the frequencies among tree species, whereas ≈21%

of the variation was due to differences among transects.

We sampled beetles by shaking trees, a method we had observed to be effective in catching ≈90% of adult beetles (Smith et al. 2001). Sampling was done over a 3-d period due to labor demands. We used the middle date for analyses and reporting purposes; for example, data sampled over 1, 2 and 3 June are collectively identified by 2 June. We counted marked (e.g., recaptured) and unmarked beetles, the latter serving as an indicator of background population abundance. We also measured the height and diameter at breast height (dbh) for all sampled trees at each sampling point to ensure that tree height and girth did not differ substantially among directions and distances. Recaptured females were dissected to detect the presence of eggs.

Across all time periods, we modeled the numbers of recaptured beetles, B_r over distance, D, using a power function,

$$B_r = AD^n, \qquad [1]$$

in which A is the trivial estimate of the y-intercept, and n is the rate of decay. Model convergence was based on the Marquardt algorithm (Marquardt 1963) in PROC NLIN (SAS Institute 1999). Differences in the dispersal rate (meters per day) between recaptured males and females, the data for which were highly skewed, were tested using the Kolmogorov–Smirnov nonparametric test (PROC NPAR1WAY, SAS Institute 1999).

Spatial and Temporal Dynamics. We used unmarked beetles from this study and unmarked beetles from our previous study in 1999 (Smith et al. 2001) to quantify temporal dynamics of *A. glabripennis* over a degree-day (DD) scale. Daily maximum and minimum temperatures for 1999 and 2000 were obtained from the National Climatic Data Center (2003) for Lanzhou, Gansu Province, China, which was located ≈60 km east of our field site and also borders the Yellow River. Because development in *A. glabripennis* is not well known over a range of temperatures, we used an arbitrary minimum base temperature threshold of 10°C. Degree-day accumulation from 1 January for each year was estimated using the sine wave method (Allen 1976). Using data from both years, we then modeled the cumulative proportion of abundance, P, over accumulated degree-days, DD, by using a Gompertz function,

$$P = \exp(-\exp(-rDD + b), \qquad [2]$$

in which r and b are the rate of increase and lag, respectively (Brown and Mayer 1988). Nonlinear convergence was based on the Marquardt algorithm (Marquardt 1963) by using PROC NLIN (SAS Institute 1999).

In 2000, we chose 200 trees from our sampling grid and used this subset to study the relationship among *A. glabripennis* emergence holes, tree size, and background population abundance. For each of the eight directions around the center release point, we randomly chose five trees from each of five distances in each direction. For each tree, we counted the number of existing *A. glabripennis* emergence holes from previous years, and then counted new emergence holes during the course of 2000. The DBH of each tree was used as an indicator of size. The distributions of the numbers of existing and new emergence holes, and the total number of unmarked *A. glabripennis* adults counted on each tree over the season, were skewed and hence transformed using $\log_{10}(y + 1)$. In one analysis, we tested the effects of tree size and existing emergence holes on the number of new emergence holes. We also tested the main effects of tree size, existing emergence holes, and new emergence holes on *A. glabripennis* abundance. In both cases, significance was based on type III sum of squares (PROC GLM, SAS Institute 1999).

We also used unmarked beetles from our current study to estimate spatial autocorrelation of *A. glabripennis* at each sampling week. The number of sampling locations in 1999 was inadequate for valid estimates of spatial autocorrelation; hence, only data from 2000, which were collected over a larger sampling grid, were used. Because the number of trees in a group differed among sampling locations, we first standardized the number of unmarked beetles at each group by considering the numbers of beetles per sampled tree. These values were then expressed as the number per sampling group. We used the median number of trees at each sampling group; thus, counts were expressed as the number of beetles per 18 trees (for sampling intervals from 1 June to 11 August) or 28 trees (for sampling intervals from 18 June to 30 September). Data were then transformed using $\log_{10}(y + 1)$. Sampling locations were spatially referenced with respect to the center of the sampling grid.

Spatial structure in *A. glabripennis* was estimated using a nonparametric spatial covariance function in S-Plus (Mathsoft 2000). This function is nonparametric in that it uses a smoothing spline to measure the correlation in density between pairs of samples over a continuous function of the distance separating samples, without assuming any functional form a priori (Bjørnstad and Falck 2001). Let δ_{ij} be the Euclidean distance between spatial locations i and j and $\rho_{ij,t}$ be the spatial autocorrelation in *A. glabripennis* abundance, z_i and z_j, at the two locations at time t,

$$\rho_{ij,t} = \frac{(z_{i,t} - \bar{z}_t)(z_{j,t} - \bar{z}_t)}{\frac{1}{M}\sum_{a=1}^{M}(z_{a,t} - \bar{z}_t)^2}, \qquad [3]$$

where $M = 78$ and is the total number of sampling locations, $\bar{z}$ represents the field-wide mean abundance at time t, and the denominator is the spatial variance of the population. Letting $\rho_t(\delta)$ be the expected spatial correlation between abundances as a function of distance, δ, the spatial covariance function, can be estimated from nonparametric regression of $\rho_{ij,t}$ against δ_{ij} according to

$$\rho_t(\delta) = \frac{\sum_{i=1}^{M}\sum_{j=i+1}^{M} K\left(\frac{\delta_{ij}}{h}\right)\rho_{ij,t}}{\sum_{i=1}^{M}\sum_{j=i+1}^{M} K\left(\frac{\delta_{ij}}{h}\right)}, \qquad [4]$$

where K is a kernel function with bandwidth h that defines curve smoothness (Härdle 1990; Hall and Patil 1994). We used a spline function as an equivalent kernel and 10 degrees of freedom for the spline estimation. Because space–time data cannot be replicated, we used the bootstrap method (500 replications) to generate confidence limits around the estimated nonparametric covariance function, and derived 95% confidence intervals as the 0.025 and 0.975% quartiles of the bootstrap distribution (Efron and Tibshirani 1993, Bjørnstad and Falck 2001). We were particularly interested in the estimate of local autocorrelation (i.e., the correlation between pairs separated by small distances) and the range of spatial dependence (i.e., the distance at which the autocorrelation is negligible) (Isaaks and Srivastava 1989). Voucher specimens have been deposited at the USDA–ARS Beneficial Insects Introduction Research Facility in Newark, DE.

Results and Discussion

We released 1,538 known and 38,422 unknown aged beetles from 15 June to 30 September 2000. In total, 395 marked beetles (147 females, 248 males) were recaptured during the duration of the study (2 June–30 September), of which 18 were of known age. Among unmarked beetles, we counted a total of 8,389 males and 8,225 females. Their seasonal dynamics is shown in Fig. 1. Using data from 1999 (Smith et al. 2001) and 2000, our model of the cumulative proportion of beetles over accumulated degree-days from 1 January predicts 50 and 90% completion at ≈950 and 1,430 DD, respectively (Fig. 1). In 2000, adults were captured during our first sampling interval (2 June), and for both years, peak abundance was observed during mid-July, when degree-day accumulations were ≈800-900.

Across all directions and distances, trees that we sampled for marked and unmarked beetles had a mean (± SD) height and dbh of 8.2 ± 2.8 m and 8.0 ± 3.3 cm, respectively. The highest mean height and dbh were measured from trees in the southeast direction (9.5 m and 9.9 cm, respectively), whereas the lowest were from trees in the southwest direction (7.3 m and 6.6 cm, respectively). We assumed that these differences in tree sizes were not large enough to be biologically important and bias dispersal behavior of *A. glabripennis.*

Dispersal of marked beetles is shown in Fig. 2. The exponential model (equation 1 predicted that 98% of beetles were recaptured at distances ≤920 m from the release point. However, we did recapture some beetles at our most outlying sampling points (1,000–1,080 m from release point). Because we began to recapture beetles at these outlying sites as early as July, we extended the boundaries of our sampling grid, when landscapes permitted, to include additional sampling points. Although these points were not included in the analyses because they were temporally and spatially incomplete, we did have some beetles recaptured at

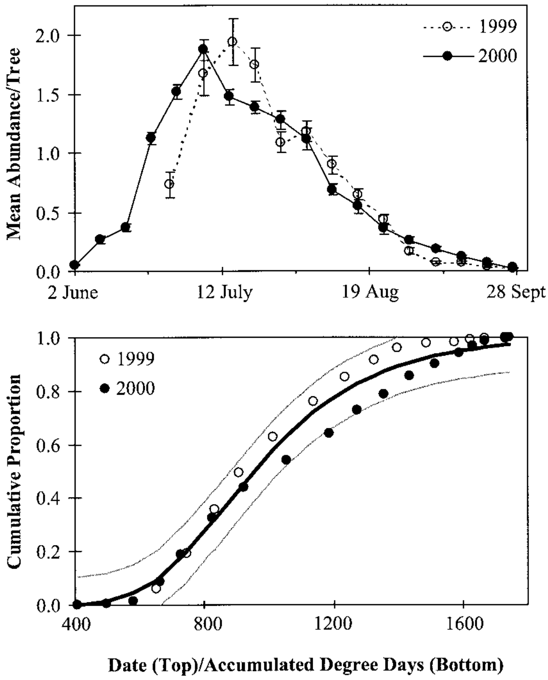

Fig. 1. Mean (±SE) population abundance of unmarked beetles in China in 1999 (from Smith et al. 2001) and 2000 (top) and cumulative proportion of beetles over accumulated degree-days from 1 January (bottom). The solid line in the bottom graph represents the model fit to both years. Predicted proportion = exp(−exp(−0.004 (±0.0002) × accumulated degree-days + 3.5 (±0.2))); R^2 = 0.88, equation 2.

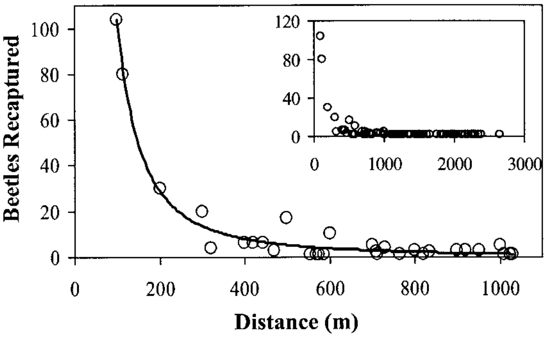

Fig. 2. Dispersal of adult *A. glabripennis.* Inset includes sampling points within the initial grid (included in the model) and locations outside the grid that were added post hoc (not included in model). Proportion recaptured = 1581(±668) × distance$^{(-1.85(\pm0.09))}$; R^2 = 0.97.

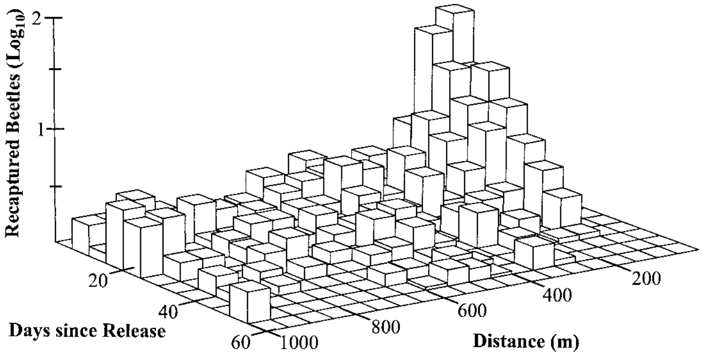

Fig. 3. Bivariate histogram of recaptured beetles over time since and distance from central release (range, 1–49 beetles).

distances up to 2,600 m from the release point (Fig. 2, inset).

The median (IQR) dispersal rates for recaptured males and females were 32.4 (12.3–55.4) and 27.5 (11.1–56.5) m/d, respectively. These rates were not significantly different ($D_{max} = 0.04$, $P = 0.8$); thus, the median dispersal rate for both sexes combined was 30.3 (11.1–55.6) m/d. These rates are different from those we reported earlier (Smith et al. 2001), in which males and females dispersed at rates of 17 and 23 m/d, respectively. However, the inclusion of sampling points farther from the release point in the current study would influence these rates. For example, one male was recaptured ≈1,280 m from the release point after only 1 d, whereas the fastest moving female went 1,340 m in 2 d. In 1999, the most outlying sampling points were 600 m from the release point, and we added no sampling points outside the original grid during the course of that study (Smith et al. 2001). Ground wind speeds recorded near the study site were very low, with an overall daily average of 1 m/s and a maximum of 3 m/s; thus, it is unlikely that the extreme displacement of some beetles in a fairly short time could be explained by ground winds. The effect of wind-assisted dispersal is not known in *A. glabripennis,* although anecdotally we have observed a behavioral response in which adults fly in an upward spiral manner when host trees are not immediately present (our unpublished data). Depending on how high up beetles will fly, it is possible that higher wind speeds above ground could facilitate movement.

A bivariate histogram of beetle dispersal over space and time is represented in Fig. 3. Roughly 93% of beetles were recaptured within 30 d, whereas three beetles were recaptured 55 d after release. Moreover, 72% of beetles were recaptured within 300 m from release, whereas 11% were recaptured at distances >600 m, or beyond the sampling radius of our previous study (Smith et al. 2001). Previous work suggests that if dispersal declines exponentially from a release point (i.e., no "fat-tailed" dispersal distributions), population spread can be quantified using the well-known diffusion equations (Kareiva 1983, Turchin 1998, Clark et al. 2001). Thus, our previous efforts (Smith et al. 2001) to model *A. glabripennis* dispersal by using diffusion approximation (Okubo 1980, Kareiva 1983, Turchin and Thoeny 1993) were not greatly biased by the additional information obtained from an increase in sampling radius used in this study. Nevertheless, the fact that some beetles can disperse at considerable distances may pose challenges to the eradication effort and particularly with regard to sampling.

If some numbers of beetles do disperse long distances, perhaps even longer than the 2,600 m that we observed, a valid concern would be the effect incipient colonies that result from long-distance dispersal events would have on eradication. Some argue that eradication of unwanted species can only be realized though the removal of all individuals (Knipling 1979, Dahlsten et al. 1989, Myers et al. 2000). However, Liebhold and Bascompte (2003) have challenged this rationale by incorporating the Allee effect (Allee et al. 1949) and stochasticity into alien species dynamics. In other words, small populations of *A. glabripennis* may not survive due to, for example, the inability to find suitable mates at low abundance, or because of disturbances, whether environmental or anthropogenic, that render habitat unsuitable.

One question concerning *A. glabripennis* movement is the ability of long-range dispersal events to initiate new colonies. In this context, we dissected recaptured females to detect the presence of eggs, and these data are presented, across both space and time, as a proportional bubbleplot (Fig. 4). Six of these females with eggs were of known ages, whereas 119 were of unknown ages. Overall, the median (IQR) number of eggs per female was five (4-7), whereas the maximum number of eggs was 13. We observed no tendency for females with eggs to be recaptured at certain distances. For example, 86% of gravid females were recaptured within the sampling grid (i.e., within 1,080 m), and 85% of all eggs were dissected from these females. Moreover, 77% of gravid females were recaptured within 600 m, as were 77% of all the eggs. There were 45 eggs removed from the eight females that dispersed >2,000 m. In the United States, survivorship of any of these eggs could result in the infestation of areas that would be outside of the current 0.8 km (0.5

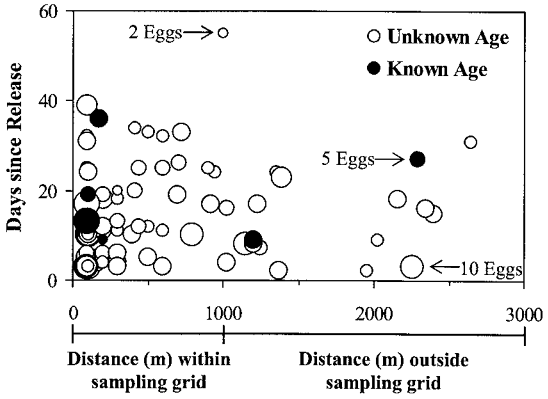

Fig. 4. Proportional bubbleplot of the number of eggs dissected from gravid females over time since and distance from center release. "Days since release" in known age recaptured beetles also indicates the beetle age.

mile) APHIS quarantine guidelines. However, to determine the effect of these incipient populations—assuming that these populations would be at low abundance—on eradication efforts, future studies should focus on the individual fitness of the offspring of *A. glabripennis* adults that traverse distances beyond the current APHIS guidelines.

Our analysis of the subset of 200 trees indicated that tree size ($F = 160.7$, df = 1,197, $P \leq 0.01$) and the number of existing emergence holes ($F = 6.3$, df = 1,197, $P \leq 0.01$) were significant predictors of the numbers of new emergence holes. The interaction between main effects was also tested and although significant, its inclusion in the model resulted in <1% difference in the model R^2 and hence was omitted. The behavior of the regression model is shown in Fig. 5. The main effects explain ≈51% of the variability in the number of new emergence holes, and the parameter estimates for both effects were positive (Fig. 5).

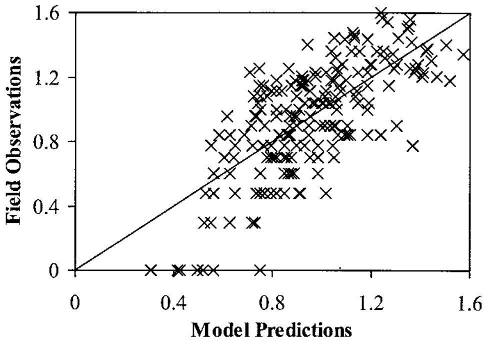

Fig. 5. Relationship between model predictions, by using the effects of tree size and the number of existing emergence holes, and observations on the number of new emergence holes. The line represents a 1:1 relationship (model predictions = 0.10 (±0.01) × DBH + 0.11 (±0.05) × $\log_{10}$(existing holes + 1); $R^2 = 0.51$, $n = 200$. The estimate for the intercept was not significantly different from 0).

Table 2. Estimates of local spatial autocorrelation and the range of spatial dependence in *A. glabripennis* in China

Sampling days	Local autocorrelation (95% CI)	Range (m) (95% CI)	Mean abundance/ tree
1–3 June	0.24 (−0.16, 0.62)	NA	0.06
8–10 June	0.35 (0.17, 0.49)	267.1 (192.5, 370.2)	0.27
15–17 June	0.55 (0.37, 0.76)	229.4 (193.7, 304.3)	0.37
22–24 June	0.30 (0.14, 0.46)	258.3 (197.6, 347.1)	1.13
29 June–1 July	0.60 (0.29, 0.78)	367.1 (252.2, 509.8)	1.52
6–8 July	0.28 (0.09, 0.44)	487.0 (199.2, 575.0)	1.87
13–15 July	0.36 (0.10, 0.54)	542.7 (444.7, 615.9)	1.47
20–22 July	0.29 (0.07, 0.46)	518.1 (173.8, 619.2)	1.38
27–29 July	0.30 (0.13, 0.41)	493.3 (318.1, 591.2)	1.28
3–5 Aug.	0.06 (−0.15, 0.25)	NA	1.11
10–12 Aug.	−0.02 (−0.23, 0.17)	NA	0.69
17–19 Aug.	0.31 (0.09, 0.47)	323.1 (257.2, 447.0)	0.54
24 Aug.–30 Sept.[a]	0.07 (−0.04, 0.18)	NA	0.17

CI, confidence interval; NA, not applicable.

[a] Estimates of local autocorrelation for weeks during this interval were nonsignificant. For simplicity, values shown are pooled means (and corresponding confidence intervals) over all weeks.

The positive relationship between tree size and new emergence holes intuitively suggests that larger trees can support more larvae. However, the positive relationship between existing emergence holes and new emergence holes may have resulted from the range of tree sizes and status of the host colonization process at the time of our study, more specifically the status of the existing emergence holes per unit tree size. In *A. glabripennis,* host colonization is a multiyear dynamic process. In other words, adults reattack their hosts over multiple years and thereby slowly kill their hosts. Thus, there is likely and intuitively an upper threshold for existing emergence holes per unit tree size at which point new exit holes would decline. Therefore, at a certain level of host quality, the rate of reattack, and consequently new emergence, will decline as beetles seek more suitable hosts.

Using this same subset of 200 trees, we did not measure a significant effect of tree size ($F = 0.32$, df = 1,196, $P = 0.57$), the number of existing emergence holes ($F = 0.02$, df = 1,196, $P = 0.92$), or the number of new emergence holes ($F = 0.06$, df = 1,196, $P = 0.80$) on *A. glabripennis* abundance. These results may suggest that recently emerged adults may not remain on the tree in which they developed (natal hosts), and/or that immigrating adults to a tree are in large enough numbers to mask any effect of the resident population. Future research is needed to address both the question of host colonization and density-dependent dispersal, specifically as a measure of host quality and population density.

Estimates of local spatial correlation and ranges of spatial dependence are presented in Table 2. During peak *A. glabripennis* abundance (i.e., mid-June to late July), we measured significant estimates of spatial autocorrelation, and the behavior of the spline correlograms over lag distance is represented in Fig. 6. The range of spatial dependence varied from week to week during peak abundance, with a mean range of 395 m

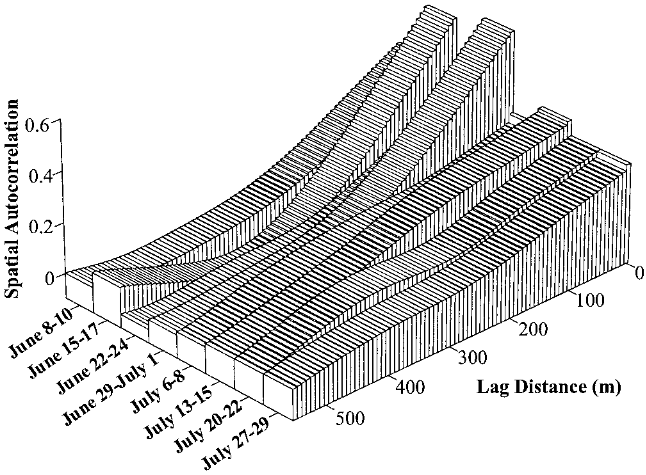

Fig. 6. Plots of the spline correlogram over lag distance during peak background population abundance.

across these sampling intervals. Furthermore, estimates of local spatial autocorrelation, which ranges from −1 (negative autocorrelation) to 1 (positive autocorrelation) averaged 0.38 across these weeks. This reveals new information regarding the spatial dynamics of *A. glabripennis* in its native habitat that could be used in spatial predictions as an exotic pest. For example, the estimates of spatial range are useful as a guide for obtaining spatially independent information during surveys. Spatial prediction algorithms can also be developed that would permit interpolation of unsampled locations of potentially infested areas around a point of known infestation.

However, in urban U.S. landscapes, these estimates of spatial pattern would likely have to be modified to include not only greater landscape heterogeneity but also the presence of anthropogenic habitat common to urban landscapes that are not suitable to *A. glabripennis.* Nevertheless, it is still likely that adults exhibit some range of spatial dependence even in the most fragmented landscapes. More work, mainly through comprehensive data exploration of the spatial and temporal dynamics of current U.S. infestations, is needed to assess key aspects of beetle spatial ecology and to relate spatial information from native habitats to U.S. landscapes.

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References Cited

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders Company, Philadelphia, PA.

Allen, J. C. 1976. A modified sine wave method for calculating degree days. Environ. Entomol. 5: 388–396.

Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions, estimating and testing. Environ. Ecol. Stat. 8: 53–70.

Brown, R. F., and D. G. Mayer. 1988. Representing cumulative germination. 2. The use of the Weibull function and other empirically derived curves. Ann. Bot. 61: 127–138.

Clark, J. S., L. Horváth, and M. Lewis. 2001. On the estimation of spread for a biological population. Stat. Prob. Lett. 51: 225–234.

Corbett, A., and R. E. Plant. 1993. Role of the movement in the response of natural enemies to agroecosystem diversification: a theoretical evaluation. Environ. Entomol. 22: 519–531.

Cressie, N.A.C. 1993. Statistics for spatial data. Wiley, New York

Dahlsten, D. L., R. Garcia, and H. Lorraine. 1989. Eradication as a pest management tool: concepts and contexts, pp. 3–15. *In* R. Garcia [ed.], Eradication of exotic pests, Yale University Press, New Haven, CT.

Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, London, England.

Fleischer, S. J., P. E. Blom, and R. Weisz. 1999. Sampling in precision IPM: when the objective is a map. Phytopathology 89: 1112–1118.

Haack, R. A., K. R. Law, V. C. Mastro, H. S. Ossenbruggen, and B. J. Raimo. 1997. New York's battle with the Asian long-horned beetle. J. For. 95: 11–15.

Hall, P., and P. Patil. 1994. Properties of nonparametric estimation of autocovariance for stationary random fields. Prob. Theory Rel. 99: 399–424.

Härdle, W. 1990. Applied nonparametric regression. Cambridge University Press, Cambridge, MA.

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

Kareiva, P. 1983. Local movements in herbivorous insects: applying a passive diffusion model to mark-recapture field experiments. Oecologia (Berl.) 57: 322–327.

Knipling, E. F. 1979. The basic principles of insect population suppression and management. U.S. Dep. Agric., Washington, DC.

Liebhold, A. M., and J. Bascompte. 2003. The Allee effect, stochastic dynamics and the eradication of alien species. Ecol. Lett. 6: 133–140.

Liebhold, A. M., R. E. Rossi, and W. P. Kemp. 1993. Geostatistics and geographic information systems in applied insect ecology. Annu. Rev. Entomol. 38: 303–327.

Marquardt, D. W. 1963. An algorithm for least squares estimation of nonlinear parameters. J. Soc. Ind. Appl. Math. 11: 431–441.

Matheron, G. 1963. Principles of geostatistics. Econ. Geol. 58: 1246–1266.

Mathsoft. 2000. S-Plus 2000 Programmer's Guide, Data Analysis Products Division, Seattle, WA.

Myers, J. H., D. Simberloff, A. M. Kuris, and J. R. Carey. 2000. Eradication revisited: dealing with exotic species. Trends Ecol. Evol. 15: 316–320.

National Climatic Data Center. 2003. (http://www.ncdc.noaa.gov).

Nowak, D. J., J. E. Pasek, R. A. Sequeira, D. E. Crane, and V. C. Mastro. 2001. Potential effect of *Anoplophora glabripennis* (Coleoptera: Cerambycidae) on urban trees in United States. J. Econ. Entomol. 94: 116–122.

Okubo, A. 1980. Diffusion and ecological problems: mathematical models. Springer, New York.

Rossi, R. E., D. J. Mulla, A. G. Journel, and E. H. Franz. 1992. Geostatistical tools for modeling and interpreting ecological spatial dependence. Ecol. Monogr. 62: 277–314.

Rudd, W. G., and R. W. Gandor. 1985. Diffusion model for insect dispersal. J. Econ. Entomol. 78: 295–301.

SAS Institute. 1999. SAS/STAT user's guide, version 8, Cary, NC.

Smith, M. T., J. Bancroft, G. Li, R. Gao, and S. Teale. 2001. Dispersal of *Anoplophora glabripennis* (Cerambycidae). Environ. Entomol. 30: 1036–1040.

Southwood, T.R.E. 1978. Ecological methods with particular reference to the study of insect populations. Chapman & Hall, London, England.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer, New York.

Turchin, P., and W. T. Thoeny. 1993. Quantifying dispersal of southern pine beetles with marked-recapture experiments and a diffusion model. Ecol. Appl. 3: 187–198.

Wen, J., Y. Li, N. Xia, and Y. Luo. 1998. Study on dispersal pattern of *Anoplophora glabripennis* adults in poplars. Acta Ecol. Sin. 18: 269–277.

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