Dispersal of *Anoplophora glabripennis* (Cerambycidae)

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ABSTRACT As a basis for the development of both eradication and management strategies for control of *Anoplophora glabripennis* Motschulsky (Asian longhorned beetle) investigations of *A. glabripennis* dispersal were undertaken in Gansu Province, China, in 1999. Data analysis of the first year study of population dispersal, in which >16,000 adult *A. glabripennis* were marked and released (mass-mark recapture method), has shown that the mean dispersal distance for *A. glabripennis* was ≈266 m, whereas the 98% *A. glabripennis* recapture radius was 560 m. More notably, *A. glabripennis* dispersal potential over a single season was found to be 1,029 m and 1,442 m, for male and gravid female beetles, respectively, which is well over the previously reported distances. There was also a directional bias in dispersal. These results indicate that surveys for adult beetles and infested trees at a minimum of 1,500 m from previously infested trees would assist in preventing continued colonization in the current U.S. infestations in New York and Chicago, and therefore enhance efforts to eradicate *A. glabripennis* from the United States. Data from the second year of this study (2000) will be used to enhance a predictive model of invasion by *A. glabripennis* in landscapes at risk in the United States.

KEY WORDS mark-recapture, diffusion, invasive species, Cerambycidae, Asian longhorned beetle

Anoplophora glabripennis Motschulsky (Asian long-horned beetle) is native to China and Korea. This invasive species was first discovered in North America in New York (New York City and Long Island) in 1996, and discovered in Chicago, IL, in 1998. *Anoplophora glabripennis* was probably introduced from solid wooden packing materials (i.e., crating, palettes, dunnage) originating from China. *Anoplophora glabripennis* larvae feed in the cambium and xylem of a large variety of hardwood tree species, including maple, willow, elm and poplar, eventually killing the entire tree.

Anoplophora glabripennis, as a recent invader, is a candidate for eradication because infestations are currently thought to be limited in size and scope. The aim of eradication is the elimination of all reproductively viable *A. glabripennis* from North America. Intensive survey for infested trees, followed by felling, removal and chipping, is currently the only available method of population suppression. Effective surveys require establishment of boundaries around infestations (referred to as quarantined and/or eradication survey boundaries), inside of which surveys are conducted. However, delineation of boundaries is based upon the dispersal potential of *A. glabripennis.* Current guidelines for Animal Plant Health Inspection Service (**APHIS**) eradication surveys are a half mile from the closest known infested tree, which are based upon rate of detection of infested trees. However, dispersal is likely the most important factor for invasion by exotic species (Higgins et al. 1996). Therefore, the study reported herein is aimed to provide critical new information on the dispersal potential of adult *A. glabripennis.* This information will provide a basis for the delineation of the quarantine boundaries and concentrating survey and detection efforts, and thereby lower the detection threshold (population level at which beetles are detected) for incipient populations.

Because the release of *A. glabripennis* is prohibited in North America, we conducted a mark recapture field experiment in Gansu Province, China, to estimate *A. glabripennis* dispersal characteristics (i.e., distance). In the event that *A. glabripennis* becomes uncontainable in the United States, this research, when coupled with other current investigations (i.e., colonization behavior, host preference, natural enemies), will provide estimates of *A. glabripennis* dispersal parameters that are applicable in other landscapes at risk (i.e., forests) in North America. In so doing, therefore, this proactive approach will form the basis for development of adaptive management strategies for this and other invasive species.

Materials and Methods

The field site was one km west of the town of Liu Hua, bordering the Yellow River in Gansu Province of north central China. This field site was selected because it possessed characteristics similar to those of the urban infestations in the United States, particularly site-specific factors that are thought to influence

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dispersal distance. The general landscape is composed of both host (72.3%) and nonhost (27.7%) tree species of mixed age classes. Known *A. glabripennis* hosts are dominated by *Populus nigra* L. variety *thevestina* (Dode) Bean, comprising ≈87% of the *A. glabripennis* hosts, followed by *Salix* sp. and *Ulmus* sp., at 9% and 4%, respectively. The study site was composed of trees planted as wind-rows (generally two m spacing within rows and 50 m spacing among rows) bordering agricultural fields, as well as isolated trees and trees planted along paths amid dwellings, such as homes and greenhouses. Greenhouses and small dwellings were also commonly found within or adjoining agricultural fields.

Anoplophora glabripennis used in this study included both newly emerged and unknown aged adults. Known-aged adult beetles were collected from poplar-tree bolts (≈1.5 m in length) transported to the center release site. Beetles were marked and released daily as they emerged from these caged bolts. In addition, beetles of unknown age were collected weekly outside the recapture area, transported to the center release site, marked and released. Beetles were marked with colored paint applied to the pronotum. Different colors were used to differentiate the time of release, newly emerged and unknown aged beetles. In addition, newly emerged beetles were marked with a different color weekly so that the age and time spent dispersing could be calculated upon recapture.

Transects radiated from the center release site in eight directions: north, northeast, east, southeast, south, southwest, west and northwest. Recapture locations lay along each transect at 50, 100, 150, 200, 250, 300, 400, 500, and 600 m from the center release site. However, due to landscape heterogeneity (presence of obstacles), recapture locations were missing at S50, S100, S250, E50, W50, W200, W400 and N50, and thus resulted in a total of 64 (not 72) recapture locations. Recapture abundance at each distance was normalized to the number of trees at each distance to account for the missing locations and locations with fewer trees.

Each recapture location was composed of a fixed group of poplar trees (average of 12 trees per location; average tree diameter at breast height (dbh) and tree height was 7.2 cm and 7.8 m, respectively). Trees at each recapture location were sampled weekly for adult *A. glabripennis* by shaking from 18 June to one October 1999. The tree shaking method employed in these studies was standardized in preexperiment trials so as to ensure consistent sampling in each recapture location. This method generally allowed catching of ≈90% of beetles in the trees, and missed beetles would have minimal effect on the resulting dispersal distribution. Each recaptured *A. glabripennis* was preserved, and the location, release date, sex, and body length and width recorded. In addition, marked female beetles were dissected and the number of mature eggs recorded. Unmarked adult beetles collected were recorded and released.

The dispersal models used to estimate dispersal are based on the well-known diffusion model (Okubo 1980). This equation has been tested in numerous studies (Shigesada and Kawasaki 1995; Turchin 1997) and is a robust approximation for ecological studies using the mass mark-recapture technique.

$$\frac{\partial n}{\partial t} = D\left(\frac{\partial^2 n}{\partial x^2} + \frac{\partial^2 n}{\partial y^2}\right) = D\left(\frac{\partial^2 n}{\partial r^2} + \frac{1}{r}\frac{\partial n}{\partial r}\right), \quad [1]$$

where n is the density of beetles, t is time; D is the diffusion coefficient, x and y are spatial coordinates, and r is the radial distance from the release site ($r = \sqrt{[x^2+y^2]}$). We are interested in the diffusion coefficient, which determines the rate at which beetles move. The key assumption of this equation is homogeneous movement across the landscape. This may be relaxed to test the significance of bias in direction of movement and variation in the diffusion parameter within the landscape. In the discussion, we describe how prevailing winds, orientation to the angle of the sun, or host-tree distribution may play a role in our results. We used three approaches to estimate dispersal based on this model. The first two approaches are based on the following solution of equation 1.

$$n(r,t) = \frac{\delta n_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt}\right), \quad [2]$$

where δ is the disappearance of beetles and n_0 is number of beetles released. Our first approach fit the diffusion coefficient directly (Kareiva 1983). For each of 8 wk from the time of release, a diffusion coefficient was calculated.

$$D = \frac{r_a^2}{\pi t} \quad [3]$$

$$r_{98} = 2\sqrt{4Dt}, \quad [4]$$

where r_a is the mean displacement of beetles for the week, and r_{98} estimates the radius that encompasses 98% of the beetles. The overall estimates are the mean of the eight estimates (one for each week) weighted by the number of recaptures during the week.

The second approach estimated both a diffusion and disappearance coefficient using the distribution of beetle abundance at the nine distances. For each of the 8 wk of data, we fitted equation 2 by minimizing the sum of squared error (least squares) in the distribution of observed beetles. By rearranging equation 3 we estimated mean displacement for each week.

$$r_a = \sqrt{\pi Dt}. \quad [5]$$

Then equation 4 was used to calculate the 98% dispersal estimate for the population.

The third and final approach used the sum of captured *A. glabripennis* across time at each distance (Turchin and Thoeny 1993). Equation 6 only depends on distance.

$$n(r) = \frac{n_0(8\pi)^{-1/2}(\delta D^3)^{-1/4}}{r^{1/2}} \exp\left(-\frac{r}{(D/\delta)^{1/2}}\right). \quad [6]$$

This diffusion and disappearance coefficients D and δ were estimated from the distribution of nine abun-
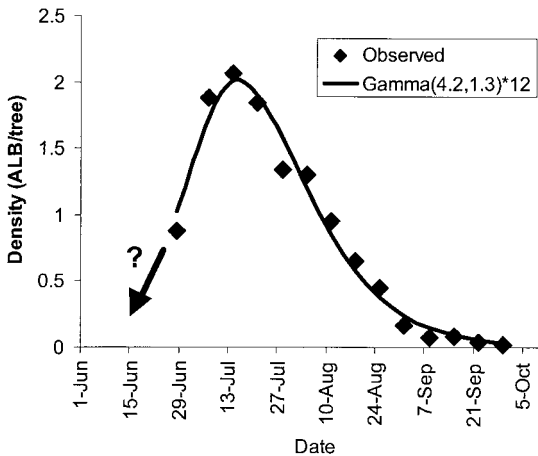
Fig. 1. Seasonal dynamics of *A. glabripennis* in Gansu Province. Average density of *A. glabripennis* per tree in 1999. *A. glabripennis* begin to emerge in early June and reach peak abundance in mid-July.

dances or distances to recapture. Finally, the mean time to recapture for all data were used in equations four and five to estimate population dispersal distance.

Analysis of variance (ANOVA) was also performed to test for bias among eight directions in distance of dispersal or in numbers of *A. glabripennis* recaptured. We also tested for differences in dispersal rate (meters/d) between sexes using the nonparametric Kolmogorov-Smirnov test (Kolmogorov 1941, Smirnov 1948, StatSoft 1999).

Results and Discussion

A total of 188 marked *A. glabripennis* were recaptured (16,511 marked beetles were released). The distribution of 7,529 captured (marked and unmarked) adult beetles shows the seasonal activity of adult *A. glabripennis* (Fig. 1). This indicates that adults begin to emerge in early June. Climatic difference between our field site and U.S. infestations probably make little difference in the *A. glabripennis* seasonal dynamics. This is based upon the seasonal dynamics of *A. glabripennis* across its very broad geographic (climatic zones) range in China (Yan 1985). Virtually all of the eastern United States has climatic zones similar to those found harboring *A. glabripennis* in China. It should be noted that the majority of adult *A. glabripennis* found in the United States have been sited and reported by the general public, and thus much effort has been directed toward enlisting the public's assistance in the eradication program. Therefore, as it pertains to *A. glabripennis* eradication efforts in the United States, these data indicate that public education concentrated in May–June, before adult emergence, would be most effective. Survey for emergence holes should be intensified after peak emergence, and continued through the fall.

Neither analysis for directional bias in distance of dispersal nor in numbers of *A. glabripennis* recaptured

showed statistically significant bias. However, anecdotal behavioral observation suggested that there was more east-west movement than north-south. Therefore, we tested for a difference in the number of recaptures between the east-west and north-south axes using the binomial distribution. This assumes a 50% probability of recapture of marked *A. glabripennis* along these axes and was applied to the observed recaptures (7 north-south versus 17 east-west recaptures). We calculated a 3.2% chance for the observed recaptures, which suggests an east-west bias. We have undertaken a flight behavior study that will better quantify any directional bias.

Surprisingly, there was no significant correlation in eggs remaining in females as distance increased. One explanation is that *A. glabripennis* emerge with their full complement of eggs, disperse to a host and then settle to oviposit. However, no female *A. glabripennis* held >25 eggs at recapture, and females are reported to be capable of producing as many as 80 eggs (R.G., unpublished data.; M.T.S., unpublished data). Therefore, this suggested that females develop eggs continuously (iteroparity). A likely reason for the lack of a relationship between number eggs remaining in *A. glabripennis* and distance is that female beetles continually produce batches of eggs (deposited singly), as seen in other cerambycids (Hanks 1998). Thus, mated females can potentially carry eggs their maximum dispersal distance.

The Kolmogorov-Smirnov test was used to test for differences between sexes because it includes differences in variance and distribution shape, as well as in mean dispersal rate (meters/d). There were 107 males and 81 females recaptured, and results suggest that there were no differences in dispersal rates between sexes (male = 17 ± 1.8 and female = 23 ± 2.8 m/d) (Dmax = 0.15; $P > 0.10$) (Fig. 2). Although the distributions of each sex appear to be similar, the dispersal rates between sexes warrant further study. In addition, however, while collecting the unknown aged beetles used in the MMR releases, 26 marked *A. glabripennis* were found outside the recapture area (13.83% of the 188 recaptured *A. glabripennis*). Because the same trees were not surveyed regularly outside the recapture area, these 26 marked *A. glabripennis* were not included in our analysis and prediction of dispersal. However, both male and gravid *A. glabripennis* were included among these 26 beetles, with maximum dispersal distances of 1,029 m and 1,442 m, respectively. This is the longest dispersal distance previously reported or observed for *A. glabripennis*.

The bivariate histogram shows the distribution *A. glabripennis* over space and time (Fig. 3). Values from this histogram were used to fit the diffusion models and estimate *A. glabripennis* dispersal. The dispersal estimates based on equation 2 (Table 1, columns a and b) show large variation, and the dispersal estimate based on equations 3 and 4 (Table 1, column c) lies between these two estimates. For the first approach, the direct calculation of the diffusion coefficient (*D*) was 544 ± 230 m. This resulted in the largest estimate of dispersal distance (column a). For the second ap-
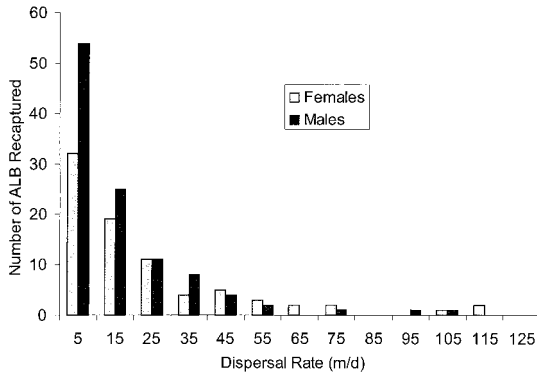
Fig. 2. Dispersal rate (meters/d) among male and female *A. glabripennis.*

Table 1. Estimates of the diffusion coefficient for *A. glabripennis*

	Estimates of diffusion coefficient		
	Approach-1 Equation 2: direct calculation	Approach-2 Equation 2: fitting method	Approach-3 Equation 3
Median dispersal distance (m)	316	192	266
98% recapture radius (m)	713	435	560

proach, the fitted parameters were $D = 1,359 \pm 1,366$ m and $\delta = 0.00870 \pm 0.00322$ m. This suggested a smaller estimate of *A. glabripennis* dispersal distance (column b). Finally, the time integrated dispersal approach was used to calculate the $D = 54.0$ and $\delta = 0.00188$. This estimate (column c) represents a judicious prediction from the available data (Fig. 4). Collectively, the three approaches provide a range for dispersal prediction and establish confidence for their use in surveys of *A. glabripennis* infestations in the United States.

Previous work suggests that <15% of beetles dispersing farther than the most distant trap will make only minor differences in predictions (Kareiva 1983). The estimation of the "tail" of the dispersal distribution is a common problem in ecology (Turchin 1997), and the diffusion model may underestimate dispersal if long distance dispersal occurs frequently. Our future studies will provide a more accurate estimate of the
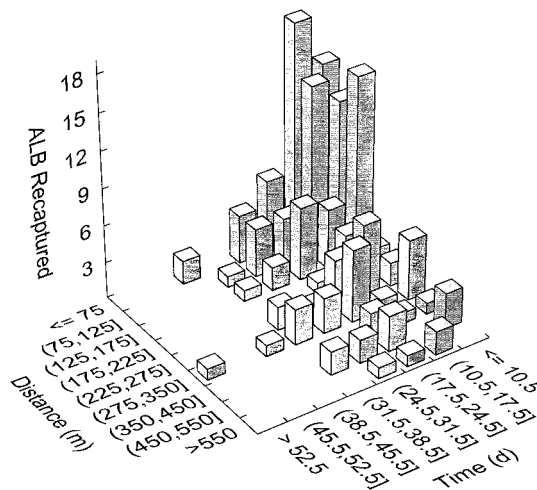
shape of the tail by acquiring a larger data set at greater distances from the release site.

Lower *A. glabripennis* dispersal distances have generally been reported than those found in the study reported here. These differences may be based upon a variety of factors. First, recapture sampling at high frequency over an extensive area may "trap out" dispersing individuals (Turchin 1997). This may have contributed, in part, to the lower average dispersal distance of 106 m reported from the mark recapture study by Wen et al. (1998), in which they recaptured *A. glabripennis* daily or every other day. Weekly recapture sampling was used in the study reported here. Secondly, recapture sampling duration, both in terms of the entire life-span of an insect, as well as across an entire season, provides a more accurate measure of population dispersal. Wen et al. (1998) used unknown-aged *A. glabripennis,* and extrapolated dispersal distance from the first 28 d of recapture. As many insects are known to decrease movement behavior with age (Aviles and Gelsey 1998; Hastings 1992; Li and Margolies 1993), this may account, in part, for their shorter dispersal distance. Both life-time (use of newly emerged *A. glabripennis*) and season-long (recaptured for ≈100 d) *A. glabripennis* dispersal potential were ascertained in the study reported here. Finally, landscape heterogeneity, especially variation in size and arrangement of tree species, is likely to have strong effects on *A. glabripennis* dispersal. This
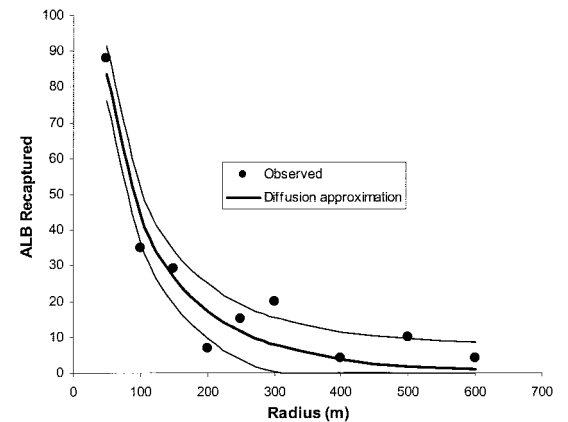

Fig. 3. Bivariate histogram of recaptured beetles over time-since and distance-from central release. The values represented in this graph were used to calibrate dispersal approximations.

Fig. 4. Diffusion approximation of *A. glabripennis* dispersal. The outer lines represent standard error.

too may account, at least in part, for the lower *A. glabripennis* dispersal distance (generally within 200 m, but not >300 m) reported by Huang (1991), where they conducted their experiment in a homogeneous young poplar plantation (3 by 5-m tree spacing). *Anoplophora glabripennis* dispersal distance may tend to be relatively low in plantations where preferred host trees are proximal, but greater where preferred host trees are more widely spaced. Our field site (described above) contained heterogeneity in key features that are likely to be important to *A. glabripennis* dispersal. Our future studies will strengthen the understanding of host tree interaction and dispersal in response to landscape elements, with particular attention to the factors that induce flight (e.g., host tree quality and species, and *A. glabripennis* population density and age).

In closing, perhaps the most notable data ascertained from this study, as it pertains to eradication of *A. glabripennis,* is that the maximum dispersal distance recorded, including that of female beetles carrying mature eggs, was 1,442 m. It must be assumed, therefore, that *A. glabripennis* have the potential to disperse at least 1,442 m in the United States. Unless monitoring or treatment of trees extend to this distance, small incipient colonies are likely to hinder eradication.

Acknowledgments

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