Dispersal and influences on movement for *Anoplophora glabripennis* calculated from individual mark-recapture

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Abstract

We conducted an individual mark-release-recapture experiment on the beetle, *Anoplophora glabripennis* Motchulsky (Coleoptera: Cerambycidae). This invasive beetle has been introduced from Asia to Europe and North America and poses a serious threat to several important species of tree. Eradication efforts may benefit from knowledge of dispersal behaviour. Trees were cut and held to determine emergence rate of *A. glabripennis*. Unique marks were painted onto 912 beetles released into a group of 165 trees in Gansu, China. Data on subsequent sightings of beetles were used in a truncated diffusion model to calculate flight distances. Characteristics of the trees and climatic information were used in statistical tests for influence on movement. A total of 2245 sightings of beetles were observed and 29% of marked beetles were resighted. The scanning technique using binoculars was 90% effective in finding beetles and provided 81% accuracy for determining the sex of the beetles. Experimental manipulation of density quantified how *A. glabripennis* congregated on unoccupied trees and were repulsed from crowded hosts. The seasonal emergence rate of adults declined exponentially from July 20 to August 5. The results suggested *A. glabripennis* fly to nearby host trees at a rate of 34% per day. Median flight distance was estimated at 20 m per day. Statistical analysis with a generalized linear model tested the beetle's propensity to leave a tree and distance of flight. Generally, beetle movement showed a significant response to beetle density, weather conditions, beetle size, and tree size, in that order. The techniques developed here improve on previous recapture techniques to quantify dispersal and can be useful for analysing populations of other organisms.

Introduction

Anoplophora glabripennis (Motschulsky) (Coleoptera: Cerambycidae) is an invasive pest with breeding populations in Saltsburg, Austria; Toronto, Canada; New York and Chicago, USA. The beetle is undergoing eradication in quarantine zones to prevent the death of more ornamental trees in these cites. The US eradication program has removed more than 7000 trees, most of which were infested. Despite a decreased rate of detection of infested trees, the total quarantine area has increased (APHIS, 2003). The cost of replacing trees in the USA alone has been projected at

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$650 million (Nowak et al., 2001), with potential losses of $41 billion (APHIS, 2003). The European community has taken precautions based on climatic suitability across southern Europe (MacLeod et al., 2002). In China, *A. glabripennis* is one of the top-ten pests (Li & Wu, 1993), and it has decimated the street trees, similar to the situation in cities of Europe and North America.

Anoplophora glabripennis has a univoltine life cycle. Beetles lay eggs singly under the bark of many trees, including maple (*Acer*), willow (*Salix*), poplar (*Populus*), and elm (*Ulmus*). Larvae generally feed on the cambium layer and pupate in the xylem (Gao et al., 1993; Bancroft et al., 2002; Morewood et al., 2003). The adults emerge the following summer, and repeated attack on a tree causes girdling, weakened branches, and creates openings for secondary infection.

Despite the recognized importance of dispersal to population dynamics (e.g., Elton, 1927; Darlington, 1957; Skellam, 1951; Okubo, 1980), the difficulty of field studies has hampered quantitative dispersal estimation. There has been renewed interest in methods of data acquisition that may be interpreted in a theoretical context (Kareiva, 1982; Shigesada & Kawasaki, 1997; Tilman & Kareiva, 1997; Turchin, 1998). One dispersal study of *A. glabripennis* measured movement on the order of a few metres (Junbao et al., 1998), but lifetime dispersal may be several hundred meters (Smith et al., 2001). We expand on these studies by using individual tracking of *A. glabripennis* and assessing the influence of several biotic and abiotic factors on beetle dispersal.

Experiments using mark-release-recapture methods are perhaps the most definitive way to measure population parameters in the field (Seber, 1982). Mark-release-recapture has been used to estimate abundance, dispersal, birth, and death (Lebreton et al., 1992; Turchin, 1998). A limitation to mark-release-recapture is that movement for a given population will vary in space and time, and predictions of movement only indicate how populations will respond in similar circumstances (Schwartz & Arnason, 1996). The influence of climate and food distribution on field dispersal has been studied for coleopterans and hymenopterous parasitoids (Waage, 1983; Hanks, 1999; Desouhant et al., 2003). When environmental factors are shown to affect the demographic parameters, the general utility of a mark-release-recapture experiment may be increased.

Individual marking of insects (Wiens et al., 1993; Crist & Wiens, 1995; Kindvall, 1999) allows experiments on a population at natural densities as opposed to the large over-abundance caused by a point release. More importantly, individual mark-release-recapture allows for tests of the effects of individual characteristics on rates of both death and dispersal. Sex, size, and other physiological traits are known to have behavioural effects in the laboratory, but their effect in the field may be different. The results of mark-release-recapture experiments provide an important bridge from laboratory to field studies. More natural field tests may provide a critical link to smaller scale studies that demonstrate demographic responses in smaller controlled experiments. For our experiment with *A. glabripennis*, the relationship to climate, host trees, and beetle state may help predict the population ecology at other infestations.

The factors influencing *A. glabripennis* dispersal in the field have not been measured. We tested the effects of climate, host tree, and characteristics of the individual beetle on the propensity to disperse and how far beetles move. Dispersal distance was also analysed with a diffusion model. Understanding *A. glabripennis* dispersal is important for predicting population spread, improving eradication surveys, and managing future introductions.
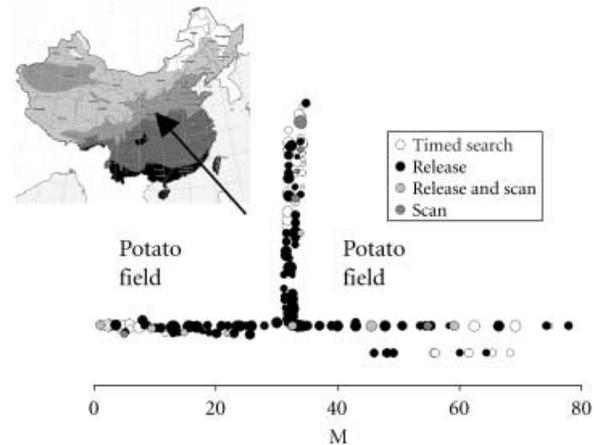
Figure 1 Map of field site showing tree locations. Tree height is represented by bubble area, and the legend shows how certain trees were used in the experiment. Inset shows field site location in Gansu, China.

Materials and methods

The field site was located in an area where *A. glabripennis* was actively expanding its range. The site was at 103.28°E, 35.96°N in the town of Liuhua, Gansu Province, China. Numerous host trees lined roads, small agricultural fields, and houses, as in areas of infestations in North America and Europe. The field site in Gansu was infested about 8 years before our study. The experimental site consisted of 165 trees that were set in a T-shape along field-crop borders (Figure 1). There were four willow (*Salix*) species, but the dominant host species was lombardy poplar, *Populus euroamericana*. The height (2.3–13 m) and architecture of the trees was conducive to resighting and collecting the beetles. We selected the field site for the broad range of tree heights, and prevalence of trees that were less than 15 cm diameter at breast height (DBH), which allowed effective shaking to capture beetles. The investigation involved three sequential release-trials of 5 days. Before a trial was to begin, healthy beetles were collected by shaking trees and capturing dislodged beetles. These collections were about 2 km from the field site and provided an abundance of healthy beetles. We marked beetles individually with up to five colours of thermoplastic paint (Dayglo Inc.), and we recorded sex and pronotum width of each beetle. The marks did not appear to affect behaviour. Birds were the only possible predators of adult beetles that were observed, and they were never seen attacking beetles. Beetles were held in jars to prevent individuals from damaging each other.

Before release of marked beetles, we cleaned each tree of almost all beetles using a standardized 'shaking' method (Smith et al., 2001). Four willow trees were less effectively

cleared of beetles. We collected unmarked beetles from all trees and recorded abundance for each tree. Marked beetles were placed on the trunk of trees and routinely crawled up into the canopy. Trees were selected for release to represent the size range throughout the field site (Figure 1). The number of beetles per tree ranged from 2–8, which was similar to the natural densities observed. The resighting procedures for the first four days of a trial were the same. We thoroughly 'scanned' 30 trees for all beetles with binoculars from several ground angles. Time limitations prevented scanning all trees each day. As for release, trees scanned were selected to represent the size range throughout the field site. We recorded the sex and colour code of all resighted beetles to estimate the abundance in a given tree. We then searched for 1 h to find as many marked beetles as we could within the site. The searching method was similar to scanning except only marked beetles were sought. This increased the resighting of marked beetles, used to estimate dispersal. Beetles that moved to another tree and returned within 24 h could not be accounted for with this technique. On day 5, the release trial was ended. A subset of trees was scanned as before, then all the trees were shaken to remove beetles. For each beetle we recorded the sex, marking colours, if present, and the tree where it resided. This procedure was performed three times on July 20–25, July 26–31, and August 1–6. Five-day trials maximised the resighting of beetles that moved, and the duration was relevant for measuring changes in natural density, dispersal, and mortality. We released a total of 912 apparently healthy *A. glabripennis*.

Descriptive statistics

Two tests measured the effectiveness of our techniques. The efficiency of the technique for estimating abundance was based on our ability to sight *A. glabripennis*. A subset of trees was scanned before the trees were shaken at the end of each of three trials, and this allowed us to compare the methods. In the second test, each beetle's sex was recorded to compare with field-observed sex. This allowed us to separate observation error and natural sex-ratio bias in the field.

Beetle mortality rate was estimated using the data from resighting and seasonal emergence. The daily emergence of beetles was observed on 205 trees that were cut from a nearby area and held upright in an enclosure. The number of beetles emerging was recorded each day, and we assume that the emergence rate was the same as that of our field site. Measurements of emergence from, and subsequent dissection of, cut logs in US quarantine zones suggest mortality was negligible (MT Smith, pers. obs.). From the daily scan data, the immigration to recently cleaned trees was estimated for unmarked beetles. When the emergence rate was removed from the appearance rate of unmarked beetles, we get an estimate of immigration,

$$\text{Appearance} - \text{emergence} = \text{immigration}. \quad (1)$$

The abundance of released beetles in our study site was similar to observed abundance of unmarked beetles shaken from the trees. Because we have not created a density gradient, we may assume equal movement into and out of the field site. When this daily migration rate was subtracted from the disappearance of marked beetles we obtain an estimate of mortality,

$$\text{Disappearance} - \text{emigration} = \text{mortality}. \quad (2)$$

This provided a mortality estimate that was specific for our site and will vary in other places and at other times.

Analysis of movement

The analysis of movement was broken into two parts. The first part consisted of four statistical tests using multiple regression that examined the effects of measured variables on movement. The first test used all resighted beetles to examine what variables increase the probability of a beetle leaving a tree. The second test used a subset of beetles that were first observed on a scan tree to test the influence of density on probability of leaving a tree. The third test used all resighted beetles to examine factors influencing dispersal distance. The final test used a subset of the data where beetle density was measured in order to examine its effect on dispersal distance. The second part of the analysis used a non-linear diffusion model to estimate population dispersal and spread (Skellam, 1951; Okubo, 1980).

Up to 11 indicator variables were used in the statistical tests. From each resighting of an individual, we calculated the distance it had moved, if any, since the previous known position. Variables used in the statistical analysis were readily measurable factors and included climatic conditions, host-tree characteristics, conspecific density, and characteristics of the individual beetle. The characteristics of the beetle were sex and pronotum width, and the number of days between sightings was also used as an indicator for movement analysis. Three weather variables were included in the analysis, which were acquired at a meteorological station 2 km away. The means for daily temperature and humidity were calculated from hourly readings throughout the day. The third weather variable was total daily rainfall in mm. The characteristics of the trees included height, DBH, and 'metres of canopy'. Metres of canopy for a poplar tree was an estimate of the linear length of the trunk covered by shoots of foliage. This technique was applied to willow trees by summing lengths of all branches over 10 cm diameter.

This was used to represent the visual cue that flying beetles may see, as well as the amount of living tissue that may provide food for beetles. These were the independent variables for the analysis.

The first two tests used a logistic regression with the independent variables to discriminate between beetles that moved to a new tree or stayed on the same tree. The analysis was performed as a binary regression with a log link so that categorical variables, sex and tree species, could be included in the analysis (Agresti, 1996). A subset of beetles was used to test the additional effect of conspecific density. This subset consisted of beetles located on scan trees that were subsequently resighted. Beetle abundance in a scan tree could then be used to test for the effect of density on the subsequent resighting. The selection of final variables in the logistic model was based on Akaike's information criterion (AIC). AIC provides a measure of model fit and penalizes candidate models for including variables that do not add explanatory power to the result (Statsoft, 1999). In this case, variables may be eliminated from the logistic regression because they do not help explain why beetles stayed or left the trees on which they were originally located.

A general linear model was used to analyse the distance of movement for each resighting. For testing the influence of trees, the dissimilarity of the three measures between two trees were used to test for an effect on movement. For example, beetles that did not depart a tree between resighting would have values of zero for tree size, DBH, and metres of canopy because the original tree did not differ from the destination tree. As stated previously, the best subset of indicator variables were selected based on variance explained with adjusted R-square (adj. R^2). As with AIC, this also penalizes models for including variables that do not add explanatory power. The use of adj. R^2 has the advantages of being a common standard for linear statistical models and may be readily interpreted as the total amount of variance explained by the model. As in the logistic regression, a test was performed on the influence of density. In this case, we tested the effect of conspecific density on resightings in a scan tree. This tested the effect of density in the current (or destination) tree on dispersal distance.

Modeling redistribution

This part of the analysis used diffusion theory to examine dispersal distance. A test for directional bias in movement could not be reliably performed because the arrangement of trees in the field site was not regular (Figure 1). Previous studies have not shown significant bias in movement direction (Smith et al., 2001). The simplest diffusion model directly calculated the diffusion coefficient (D) for each day since the beetles were released (Turchin, 1998, p. 181).

The solution for the two-dimensional case is

$$D = x^2/4t, \tag{3}$$

where x is the distance from the release point and t is days since release. From this calculation, the median distance,

$$R_a = \mathrm{sqrt}(4Dt), \tag{4}$$

and the radius that encompasses 98% of dispersing beetles is

$$R_{98} = 2\,\mathrm{sqrt}(4Dt). \tag{5}$$

This is a well-described and accurate method for most recapture studies, but when more than 10% of the organisms move beyond the most distant capture annulus, a correction may be needed (Kareiva, 1983). Because the beetles could readily fly out of the field site, a modified form was used to account for emigrating beetles. This diffusion model truncates the dispersal curve (Kareiva, 1983). The result is based on the exponentially bounded normal curve, but the probabilistic distribution (P) is used in the model fit.

$$P[x,t] = \exp[-x/(4Dt)] \Big/ \sum_0^L \exp[-x/(4Dt)] \tag{6}$$

where L is the maximum distance of recapture and all other symbols are as before. This model accounts for dispersal out of the field site while incorporating diffusion theory and the ready biological interpretation of D. A few steps were required to compare models. The natural log of the observed and calculated distributions for the 5 days were subtracted and squared. The sum of squared error was computed to get a fair measure of error for all days.

The speed of population spread has been reliably estimated using diffusion coefficient and intrinsic rate of increase. The appropriate rate for our analysis (Okubo, 1980) may be estimated as

$$c = 2\,\mathrm{sqrt}(rD_{an}), \tag{7}$$

where D_{an} is the annualised diffusion coefficient and r is the annual intrinsic rate of increase (Skellam, 1951; Okubo, 1980).

To calculate the spread of *A. glabripennis*, we used estimates of the longevity, s = 30 days, and intrinsic rate of increase, r = 3.0, from previous studies (Smith & Bancroft, 2002). From these estimates, the annualised diffusion coefficient was calculated as
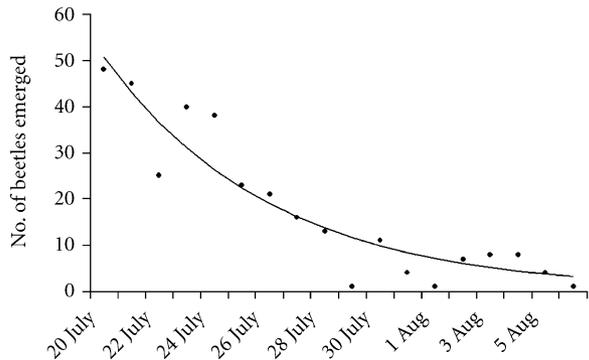
$$D_{an} = D \star s, \tag{8}$$

where s = 30 days and is the mean survival time of adult *A. glabripennis*. Finally, the intrinsic rate of increase for

A. glabripennis was used to calculate speed of population spread using equation (7). As in the description of mortality, the equation only provides a rough estimate based on conditions at our field site, and rate of invasion may vary elsewhere.

Results

The effectiveness of determining sex and estimating abundance were tested to provide a measure of confidence in the techniques. Scanning and shaking were 90% (± 4% SE) and 69% (± 10% SE) effective at acquiring unmarked beetles, respectively. Marked beetles were much easier to see while scanning because of their bright colour markings. Shaking was generally less effective and its effectiveness was likely to decrease with tree size. We tested our ability to identify a beetle's sex in the field by comparing the sex of a resighted beetle and the correct sex when the beetle was originally marked. The sex of resighted beetles was incorrect for 57 of 291 females and 58 of 321 males. This is an accuracy of 81% in the field, and there is no evidence of bias in error between the sexes ($\chi^2 = 0.04$, d.f. = 1, P = 0.83). The directionality of flight could not be reliably tested because the trees were not in a uniform distribution. The chosen site had a linear arrangement of trees similar to street trees found in sites where the beetle has invaded in Europe and North America. In addition, the arrangement allowed sighting of beetles from a low angle that was important for seeing beetles resting on upper leaf surfaces.

The daily rate of adult emergence from 205 trees fit an exponential distribution (Figure 2). The emergence rate declined from a beetle for every four trees on July 20 to one for every 50 trees on August 6. Using the scan data from the final day of each trial, we calculated the mean (± SE) density of adult beetles per tree as 2.44 ± 0.25 and density per metre of tree canopy as 0.72 ± 0.033. The size of beetles was 5.38 ± 0.04 mm and 5.90 ± 0.04 mm for males and
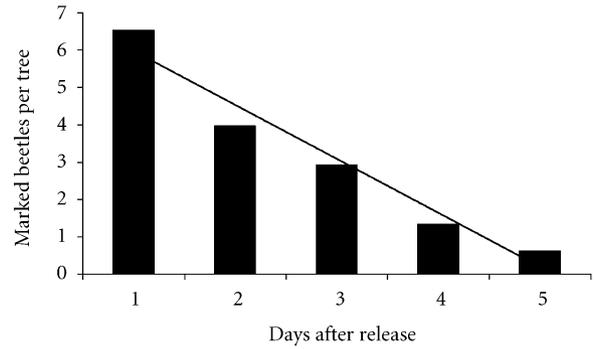
Figure 3 Disappearance (mortality and emigration) of marked *Anaplophora glabripennis* beetles pooled from three trials. Linear regression shows trend.

females, respectively. Males were smaller than females (F = 81, d.f. = 610, P<0.01).

We recorded observations on 2234 beetles. Marked beetles accounted for 746 of the resightings and of these, 612 were individually identified (we did not read all five colour marks on 134). The 612 resightings were from 375 individual beetles. The distribution of resighting frequency for individual beetles shows the rate at which they left the site by dispersal or death (Figure 3). The 375 resighted beetles represent 29% of the 912 released beetles. One beetle was sighted on 7 different days over a 14-day period. This beetle was, however, not captured by the tree-shaking method. A total of 1499 unmarked beetles were recorded by scanning trees. The sex ratio of *A. glabripennis* was 1.14 m:f, and a χ^2 test suggests the slight male bias is statistically significant ($\chi^2 = 5.32$, d.f. = 1, P = 0.02).

We calculated rates for migration and mortality using equations (1) and (2). Each of the daily values was calculated based on average abundance per tree. From the scan trees, the average appearance of unmarked beetles was 0.70 ± 0.21/tree/day. We used the 612 marked beetles to calculate the average disappearance of marked beetles as 0.76 ± 0.35/ tree/day. These values should be equal if the two following assumptions are met: first, beetles emerge from the field site's trees at the same rate as from surrounding trees. Second, unmarked beetles migrate into the site at the same rate as the marked ones migrate out. The field site and surrounding area were composed of small farm fields that were surrounded by infested poplar trees. By subtracting the emergence (Figure 2) from the appearance of unmarked beetles, the migration rate was calculated as 0.48 ± 0.18/ tree/day. Finally, removing migration from disappearing marked beetles suggests a mortality of 0.32 ± 0.19/tree/day.

Probability of moving

There were 229 beetles that did not move from the tree on which they were last recorded, while 369 moved to a new

Figure 2 Seasonal emergence of *Anaplophora glabripennis* from 205 trees. Negative exponential curve added to show trend.

A.

Parameter	Estimate	SE	Wald stat.	P
Rel time	−0.46	0.07	46.20	<0.01
Rel hum	−0.04	0.01	10.57	<0.01
No rel	0.29	0.04	51.90	<0.01
Av temp	−0.09	0.03	7.40	0.01
PN width	0.19	0.13	2.19	0.14

B.

Parameter	Estimate	SE	Wald stat.	P
No rel	0.43	0.08	29.34	<0.01
Orig ht	−0.15	0.05	8.13	<0.01
Density	−0.18	0.07	6.52	0.01
Rel hum	−0.08	0.03	5.45	0.02
Orig can	0.17	0.08	4.29	0.04
Rel time	−0.29	0.16	3.36	0.07
Av temp	−0.10	0.05	3.88	0.05
Rainfall	0.52	0.34	2.29	0.13

C.

Parameter	Estimate	SE	F	P
Rel time	0.55	0.08	51.90	<0.01
Av temp	0.10	0.03	8.16	<0.01
Rel hum	0.05	0.01	13.68	<0.01
No rel	−0.45	0.04	108.23	<0.01
Sex	1.06	0.36	8.44	<0.01
Ht diff	−0.05	0.03	2.69	0.10

D.

Parameter	Estimate	SE	F	P
No rel	−0.61	0.09	47.41	<0.01
Ht diff	−0.29	0.11	6.30	0.01
Density	0.19	0.08	5.62	0.02
Sex	0.43	0.22	3.88	0.05
Rel time	0.38	0.19	3.75	0.05
Rel hum	0.06	0.03	3.41	0.07
PN width	−0.50	0.29	2.93	0.09
Av temp	0.11	0.07	2.86	0.09
DBH diff	0.12	0.10	1.38	0.24

Table 1 Results of four statistical analyses that calculated the best subset of factors associated with dispersal in *Anaplophora glabripennis*. See text for detailed descriptions of the following indicator variables. 'Rel time' is time since beetle was last sighted. 'Rel hum' is relative humidity. 'No rel' is number of beetles released on to the tree. 'Av temp' is average temperature for the day. 'PN width' is pronotum width of the beetle. 'Orig ht' is the height of the tree on which the beetle was last resighted. 'Density' is the number of beetles in the tree, determined by scanning. 'Orig can' is the size of the tree canopy. 'Ht diff' is the difference in height between the trees with a beetle's resighting. 'Sex' is the sex of the beetle. 'DBH diff' is the difference in diameter between the trees with a beetle's resighting. All parameters have one degree of freedom. A. Multiple regression for probability of moving from tree DBH of last resighting using log link. B. Multiple regression for probability of moving from tree of last resighting on trees with density estimates using logistic link. C. Multiple regression of distance for all resightings. D. Multiple regression for distance of resightings on trees with density estimates

tree (62%). Table 1A shows the five factors that were included in the final model (AIC = 652.7). An increasing probability of moving was associated with an increasing release number on the tree, decreasing time since release, decreasing temperature, decreasing relative humidity, and increasing beetle size. We note that the second best model was very close in fit to the best subsets of parameters (AIC = 562.8). This model replaced beetle size with the beetle sex (W = 2.1, d.f. = 1, P = 0.15), with females having greater probability of moving. Neither sex nor size was a strong indicator on its own (both P>0.05). The variables eliminated from the model were tree height, size of tree canopy, tree DBH, tree species, and rainfall.

The same analysis was performed on a subset of scanned trees. This allowed inclusion of a direct observation of beetle abundance to be included in the analysis. In all, 122 beetles moved and 94 did not. The best fitting model had eight variables (AIC = 259.3). An increased probability of dispersal was observed with increasing number released into the tree, decreasing average temperature, increasing total rainfall, decreasing relative humidity, decreasing tree height, increasing canopy of the tree, decreasing beetle
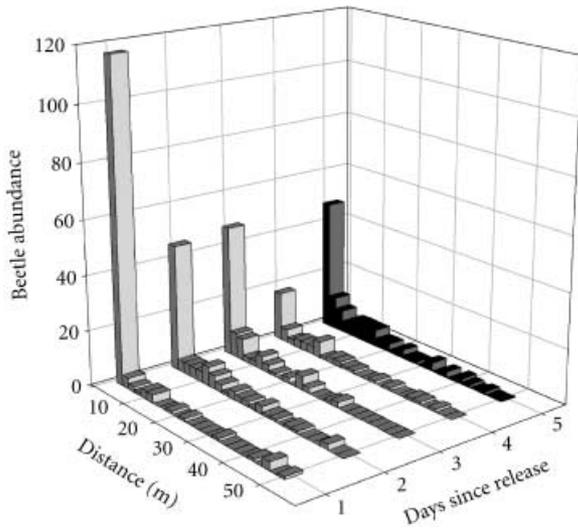
Figure 4 Histogram of resighted *Anaplophora glabripennis* beetles in response to dispersal distance and time since release or last resighting. Captures from trees using the scanning (days 1–4) and shaking methods (day 5).

density, and decreasing time since release. Variables eliminated from the model were tree DBH, pronotum width, beetle sex, and tree species.

Factors influencing dispersal distance

A total of 598 observed dispersal events were tested for environmental influence. A histogram of the recapture data shows the response to time since last recapture and distance (Figure 4). A natural log transformation was used to normalize the distribution of distances. The general linear model selected the best subset of parameters, retaining six parameters (adj. $R^2 = 0.29$). Factors associated with increased dispersal distance were increasing time since last sighting, increasing average temperature, increasing relative humidity, decreasing difference in tree heights, and decreasing release number. Difference in tree height, DBH, and metres of canopy were used to capture the effects of variation in originating and destination (or resighting) tree. For the categorical variables, increased dispersal distance was associated with female beetles (vs. males). Variables dropped from the model were pronotum width, species of destination tree, difference in DBH, and difference in metres of canopy.

The final statistical model analysed the natural log of 216 dispersal distances. The best fitting model had nine variables (adj. $R^2 = 0.24$). Increasing dispersal distance was associated with decreasing pronotum width, increasing released number, increasing average temperature, increasing relative humidity, decreasing height difference, decreasing

DBH difference, increasing density, increasing time since last sighting. Finally, the categorical variable sex was held in the model, with females flying farther. Variables dropped from the model include metres of canopy and species of tree.

Dispersal distribution fitting

Several non-linear models (Equations 3–7) were used to determine which model best described the dispersal data. The results from the diffusion models are shown in Table 2. The standard model used a direct fitting method (SSE = 1.206) and shows lower values because the exponential tail cannot capture the relatively rare long distance movements of beetles. The radius that encompassed 98% of dispersing beetles each day was from the truncated diffusion model ($r_{98} = 41$ m). For this model, the diffusion estimate using truncated normal curves fit better (SSE = 0.930), and its ability to account for truncated sampling significantly improved on the standard diffusion fit. Finally, this suggested a speed of natural spread of 129 m year^{-1}.

Discussion

The results show strong evidence for density-dependent dispersal (Table 1). Tests for probability of movement from a tree and dispersal distance indicated that *A. glabripennis* moved in response to the number of beetles released on the tree. The increasing abundance of released beetles seemed to increase emigration from a tree, but only short distance dispersal. The influence of density was expected although it is difficult to detect in field populations (Huffaker et al., 1984). The field site was in an area of active invasion with an abundance of host trees for the beetles. Coefficient estimates for density in scan trees had the opposite sign and lower value than coefficients for number released (Table 1). One hypothesis is that the presence of a few beetles is desirable, perhaps for mating. On some trees, we released eight *A. glabripennis* and may have caused competitive interference and emigration.

Beetle and tree characteristics had a relatively small influence on dispersal (Table 1). For hosts, the primary factor associated with movement was the tree's height or in the analysis of dispersal distance, height difference. There was a large variation in tree heights (2.3–13.0 m) that improved the

Table 2 Results of analysis to estimate diffusion coefficients (D), dispersal rate (r_a), 98% dispersal confidence interval (r_{98}), and speed of population invasion (c). Values include ± SE

Method	D (m d^{-1}*d)	r_a (m d^{-1})	r_{98} (m d^{-1})	c (m year^{-1})
Direct	16.2 ± 2.9	15.5 ± 1.2	25.5 ± 2.0	76
Truncated	46.4 ± 13.0	22.5 ± 5.6	45.1 ± 11.3	129

detection of significant effects on dispersal. Beetle characteristics showed a larger effect on dispersal distance than characteristics of the trees. Females and smaller beetles moved greater distances. Further studies may explain how beetle size influences mating history and competitive interference, which in turn, may effect dispersal. The effect of sex of the beetle is discussed below in the context of sex ratio variation.

The effect that time since the last resighting had on movement provides insight into dispersal behaviour. The effect of time on dispersal distance may differentiate directed and haphazard movement. Because the Poisson distribution fits movement rate (m/day) there is little reason to suspect strong directed movement to specific trees (French et al., 1968). Flying *A. glabripennis* orient toward large lush trees (JS Bancroft, pers. obs.), but the data from our field site do not suggest strong directed flight toward volatiles from a host or potential mate. Increasing time since last resighting had a negative effect on probability of leaving a tree and a positive effect on distance (Table 1). We hypothesize that if some beetles found trees highly suitable for mating and oviposition, then they would be less likely to move over time. The increase in resighting distance over time may be attributed to the search for mates, food, or places to lay eggs. This increasing displacement is expected for an organism without a territory or permanent settling (Turchin, 1998).

Variables related to weather had a weaker effect than time since last resighting, but influenced movement in a predictable way (Tables 1A and B vs. C and D). The propensity for a beetle to move lowered with increasing temperature, but distance increased with temperature. The daily average temperature and humidity at 14:00 hours were 32 °C and 51%, respectively. We observed many beetles resting under leaves on hot days. At higher temperature or humidity, we hypothesize that beetles sought refuge from the sun in foliage. However, because beetles need to warm up before flight (Keena & Major, 2001), their ability to initiate a controlled flight is improved in warmer condition. This is also why we chose to shake trees in the early morning (when temperatures were <20 °C), to capture beetles in torpor. Resting beetles typically glide downward and may intercept another tree, but warmed beetles readily make orienting turns toward distant trees (MT Smith, pers.obs.).

The dispersal flights in Figure 4 may be caused by directed movement. Daytime flights by individual beetles suggest taxis toward large canopy trees. A competing, although not mutually exclusive, interpretation suggests that there are two subpopulations with short and long distance dispersers (Inoue, 1978; James, 1978). There was no basis in our study for arbitrarily splitting the population into cryptic subpopulations, although future studies may address this. Therefore, we elected to compare the more simple diffusion

models. Yet another compelling explanation is that behaviour of some organisms at habitat edges may cause leptokurtic distributions (Morales, 2002). Ovaskainen and Cornell (2003) fitted models with edge mediated dispersal and found diffusion models captured population redistribution well. An analysis by Bailey et al. (2003) tested for non-random dispersal by accounting for the reduced opportunity of grasshoppers to be resighted when near borders of a search area. Unfortunately, the variation in host-tree distribution at our site prevented this analysis. There were few trees in the immediate vicinity of our field site, but other windrows were across each field (ca. 80 m). Accounting for emigration of beetles sighted near a border would provide an important test for a fat-tailed dispersal distribution. Our field site was chosen to mimic suburban street trees and could be considered edge habitat, and beetle movement behaviour remains unknown in more dense stands. The technique of Bailey et al. (2003) would be useful in a large forest to assess *A. glabripennis* movement. Finally, further study of the effect of non-host trees on dispersal would be valuable for managing *A. glabripennis* in mixed forests. We encourage further investigations of how the observed distribution of distances is affected by genetics, physiological state, or the spatial distribution of host trees. Ultimately, this study found a diffusion rate consistent with previous studies of lifetime dispersal (Smith et al., 2001).

The results may be used to characterize daily movement and population spread. The daily movement may average 20 m per day for an individual, but if the movement is random (along a compass direction) the annual spread of the population is not very large. The natural population spread for *A. glabripennis* may be expected to be about 100 m per year. The dispersal distribution and low R^2 values show that other factors are important in determining movement by *A. glabripennis*. These factors are likely to have non-linear effects on dispersal distance, such as physiological thresholds that induce behavioural changes in movement. In general, prediction of movement could be strengthened with stronger analytic tools that integrate causative mechanisms into models of population spread.

The movement of unmarked beetles shows several patterns. The large influx of beetles to the field site after shaking trees may be described as a 'pantry effect' (Ford & Pitelka, 1984). Beetles immigrating to suitable and empty trees are likely to stay. Also, the abundance of unmarked beetles that were shaken from trees suggests a decline in abundance over successive trials (Figure 5). In addition, the analysis of beetle disappearance showed roughly equal mortality and migration rates. Because the migration was natural and uncontrolled, extrapolation to absolute numbers of migrants would vary under differing conditions. In the USA, invasion by *A. glabripennis* shows considerable
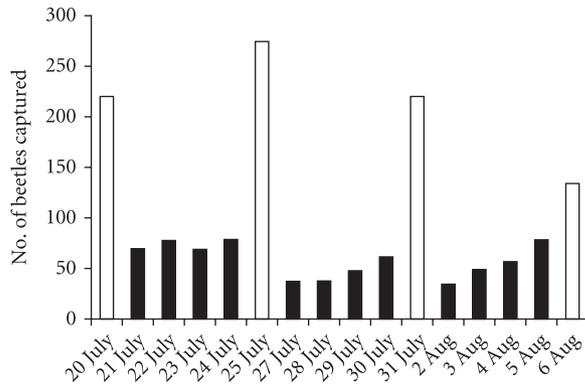
Figure 5 Raw abundance of unmarked *Anoplophora glabripennis.* Captures from trees using shaking (white bars) and scanning methods (grey bars).

variation in terms of host species and health of host trees on which they oviposit (Haugen, 2003).

The management of population spread by *A. glabripennis* may be better understood with research into how females' oviposition decisions on host trees affect sex ratios and population dynamics. In our study, the slight male bias may be the result of differences in behaviour between sexes that allowed greater sighting of the males. This differential behaviour may be exploited to disrupt mating by *A. glabripennis.* However, insects are known to manipulate offspring sex ratio depending on resource availability (Myers et al., 1998; Hardy, 2002; West et al., 2002). Further research into resource assessment by gravid females may identify ways to reduce reproduction in Europe and North America. Another hypothesis is that cycles of feeding, ovipositing, and moving may exist. Observations of oviposition suggest beetles lay a series of eggs without feeding, and study of behaviour and physiology may discover the pattern of how batches of immature beetles develop inside trees (Smith & Bancroft, 2002). The physiological cycle in a female could also affect dispersal behaviour, reducing emigration from trees perceived of high quality and synchronizing emigration from trees perceived to be of poor quality. As found in many other species, poor food resources may cause reductions in male size and an increase in male sex-ratio bias (Hardy, 2002). We observed smaller sized males in our study. Future studies with *A. glabripennis* may test the competing hypotheses concerning sex differences and their effects on population dynamics.

This paper may be summarized with three points. First, it provides an estimate of population spread by *A. glabripennis*, by using estimated rates of reproduction and dispersal. The dispersal distances and reproductive success will vary depending on climate and host-tree distribution. Second, we quantify the association between various key factors

and beetle movement. Third, our approach provides an empirical method to rapidly assess factors influencing dispersal. The technique is inexpensive, the main costs being binoculars and semi-skilled labour. The novel method we described may be applicable for studying this new cadre of cerambycid invaders (Hanks et al., 1998; Pasek, 1999; APHIS, 2003) or other systems with individually marked organisms.

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