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SHORT COMMUNICATION

Dispersal of the emerald ash borer, *Agrilus planipennis*, in newly-colonized sites

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Abstract

1 Emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is an invasive forest insect pest threatening more than 8 billion ash (*Fraxinus* spp.) trees in North America. Development of effective survey methods and strategies to slow the spread of *A. planipennis* requires an understanding of dispersal, particularly in recently established satellite populations.

2 We assessed the dispersal of *A. planipennis* beetles over a single generation at two sites by intensively sampling ash trees at known distances from infested ash logs, the point source of the infestations. Larval density was recorded from more than 100 trees at each site.

3 Density of *A. planipennis* larvae by distance for one site was fit to the Ricker function, inverse power function, and the negative exponential function using a maximum likelihood approach. The prediction of the best model, a negative exponential function, was compared with the results from both sites.

4 The present study demonstrates that larval densities rapidly declined with distance, and that most larvae (88.9 and 90.3%) were on trees within 100 m of the emergence point of the adults at each site. The larval distribution pattern observed at both sites was adequately described by the negative exponential function.

Keywords Biological invasions, Buprestidae, insect dispersal, invasive forest pest.

Introduction

Dispersal of invasive species is often characterized by stratified processes (Shigesada & Kawasaki, 1997; Liebhold & Tobin, 2008), whereby invasion spread includes a combination of short and long-distance dispersal. Long-distance dispersal events are relatively rare but serve to initiate satellite populations, which can greatly increase the rate of spread (Shigesada & Kawasaki, 1997; Liebhold & Tobin, 2008). The likelihood that a long-distance dispersal event will lead to the establishment of a satellite population requires the founding population to overcome demographic and environmental stochasticity as well as Allee effects (Liebhold & Tobin, 2008). The probability that a satellite population will become established is greatly increased when most dispersal distances are low (Robinet & Liebhold, 2009).

Dozens of isolated satellite populations of an invasive phloem-feeding beetle native to Asia, the emerald ash borer *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), have been identified across Michigan, nine other states and two Canadian provinces (Cappaert *et al*., 2005; EAB info, 2009). The emerald ash borer, a devastating pest of ash (*Fraxinus* spp.) trees, was first discovered in North America in southeast Michigan, U.S.A., and Windsor, Ontario, Canada, in 2002 (Cappaert *et al*., 2005). Efforts to mitigate the profound economic and ecological impacts associated with *A. planipennis* will most likely focus on satellite populations, although a better understanding of *A. planipennis* dispersal is critically needed if such efforts are to be successful.

Evaluating *A. planipennis* dispersal is difficult because trees with low densities of larvae typically exhibit no external symptoms (McCullough *et al*., 2009). Determining the presence of

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A. planipennis in low-density populations requires debarking trees, which is a destructive and labour intensive process. In the present study, we felled and debarked ash trees growing out to 500 m from a point source of infestations at two sites. Larval densities by distance to the epicenter were fit to a dispersal model to estimate the spread of low-density *A. planipennis* populations.

Materials and methods

Site 1

Agrilus planipennis dispersal was assessed at a weigh station for commercial trucks in Livingston County, Michigan, U.S.A. Green ash (*F. pennsylvanica*) trees were abundant in a narrow strip of land (<50 m in width) and concentrated along a 250-m stretch with very few ash trees beyond that point, and surrounded by agricultural land in three directions and a major expressway to the north. Intensive visual examination and preliminary sampling in May 2006 revealed no larval galleries, exit holes, woodpecker holes or other evidence of *A. planipennis* infestation. In addition, during the course of the study, no galleries from previous years were detected, further indicating that an infestation was not present prior to the start of this study. We stacked 20–25 infested ash logs (0.3–0.8 m long) at one end of the ash tree corridor to create a point source of emerging adult beetles. Existing exit holes on these logs were marked prior to being placed in the study site and, in late summer, well after beetle emergence was completed, logs were retrieved and new exit holes were counted. A total of 702 beetles emerged from the stacked logs. Between October 2006 and January 2007, all ash trees within 300 m of the origin ($n = 110$) were felled and sampled by debarking the trunk and major branches $\geqslant$2.5–4 cm in diameter, and recording the number of larval galleries present.

Site 2

An *A. planipennis* infestation was discovered near Tipton, Lenawee Co., Michigan, U.S.A., in autumn 2002 by regulatory officials who observed infested ash firewood piled alongside a drainage ditch in May 2002. On the basis of the amount of heavily infested ash in the pile, we estimated that 350–700 beetles emerged from the firewood. Both sides of the ditch were bordered by 50–150-m wide wooded areas with abundant green ash trees. The wooded borders were surrounded by agricultural fields, effectively creating a bidirectional corridor. Ash trees out to 500 m from the infested firewood were marked and numbered, and the diameter at breast height was measured. Up to four ash trees within 50-m interval along the ditch in both directions were randomly selected from this list for our primary sampling ($n = 64$). Available resources enabled us to sample more trees, and an additional 28 trees were randomly selected from throughout the site to increase the resolution. All 92 trees were felled and sampled on 11 February 2003 by debarking a minimum of four areas, each $\geq$2400 cm^2, spaced evenly from 1.5 m above the ground to the upper canopy (diameter >3–4 cm). This site was detected several kilometers away from the edge of the invasion wave in 2002 and all *A. planipennis* larval galleries found were 1-year galleries; therefore, the distribution of galleries at this site represents the progeny of the single generation of adult *A. planipennis* that emerged from the firewood.

An additional 23 ash trees were felled and sampled a few days later. These trees were in a woodlot located 700–850 m from the point source to the north of the agricultural field that was adjacent to the ditch. After these trees were sampled, regulatory officials destroyed all remaining ash trees within an 800-m radius of the firewood pile, in an effort to eradicate this isolated infestation.

Model fitting

For each site, the number of larvae found were summed in 10-m intervals defined by their median distance from the origin, such that '0' was defined as 5 m from the origin in both directions along the corridors, '10' as 5–15 m from the origin, etc. To correct for differences in the quantity and size of trees sampled for each 10-m interval, larval densities were calculated for each 10-m interval by dividing the total larval counts for by the m^2 of phloem sampled. Subsequently, for each site, the corrected proportion of larvae found at each interval was calculated by dividing the larval density at each 10-m interval by the sum of the larval densities throughout the site. We fit three models including the standard Ricker function (RF), the negative exponential function (NEF) and the inverse power function (IPF) (Table 1) to the data collected from Site 1 using a maximum likelihood approach, as described by Bolker (2009). Maximum likelihood was implemented in the bbmle package (Bolker, 2008) for the statistical package R (R Development Core Team, 2008). Confidence intervals for parameter estimates and corrected Akaike Information Criterion (AICc) were estimated for all models to aid in model selection. Once the best model was selected, the fit was further inspected by contrasting the predicted and observed results for Site 1.

Table 1 Parameter estimates with 95% confidence intervals (CI) for the Ricker function (Ricker), negative exponential function (NEF), and inverse power function (IPF) fit to the *Agrilus planipennis* percent larvae per 10-m interval observed at the Site 1

	Model	a (95% CI)	b (95% CI)	AICc
Ricker	ade^{-bd}	2.93 (2.42–3.51)	0.072 (0.064–0.080)	949.5
NEF	ae^{-bd}	27.08 (25.31–28.88)	0.037 (0.033–0.042)	117.7
IPF	ad^{-b}	8.84 (8.20–9.47)	0.175 (0.16–0.19)	321.5

'*d*' represents distance (m) from the origin in meters and '*a*' and '*b*' are the estimated parameters.
AICc, corrected Akaike Information Criterion.

To test the model predictions for the best model (NEF; see Results and Discussion), we compared the predicted *A. planipennis* dispersal from the model developed using the Site 1 data with the observed distribution of *A. planipennis* larval galleries recorded at Site 2. Ash trees were not present in some distance intervals at Site 2 and were not represented in our sampling (110, 120, 160, 190, 300, 340–360 and 400–440-m intervals).

Results

Of the 110 trees sampled at Site 1, 93 were positive for the presence of *A. planipennis,* and 42 of the 92 trees sampled at the Site 2 were positive. In Site 1, a total of 4520 larvae were found and the maximum density found at any interval was 63.5 larvae/m^2. Fewer larvae were found at Site 2 ($n = 346$ larvae) and the maximum density found at a single interval was also lower (24 larvae/m^2). Distribution of larvae at both sites indicated that most females oviposited on trees within 100 m of their emergence point. After correcting for sampling effort, 88.9% and 90.3% of the larvae were within 100 m of the point source, and 100% and 97.8% were within 300 m at Sites 1 and 2, respectively. The furthest distance a larval gallery was detected at Site 1 was 240 m from the origin, and 387 m along the corridor at Site 2 during the main sampling effort. However, when the 23 additional trees were sampled at Site 2, a single larva was found on a tree located 750 m from the origin.

Parameter estimates for the RF, NEF and IPF functions derived from the weigh station data with confidence intervals are summarized in Table 1. Of the models fit, the NEF had the lowest AICc value (Table 1) and provided an excellent visual fit to the data from both Site 1 (Fig. 1A), which was the site used for parameter estimation, and from Site 2 (Fig. 1B). Not surprisingly, paired t-tests failed to detect any significant differences between the predicted and observed data for either site (Site 1: $t_{18} = 1.47$, $P = 0.16$; Site 2: $t_{32} = 0.61$, $P = 0.55$), and linear regressions indicated strong relationships between the observed and predicted data (Site 1: $F_{1,17} = 227.2$, $P < 0.001$, $r^2 = 0.93$; Site 2: $F_{1,31} = 50.1$, $P < 0.001$, $r^2 = 0.61$).

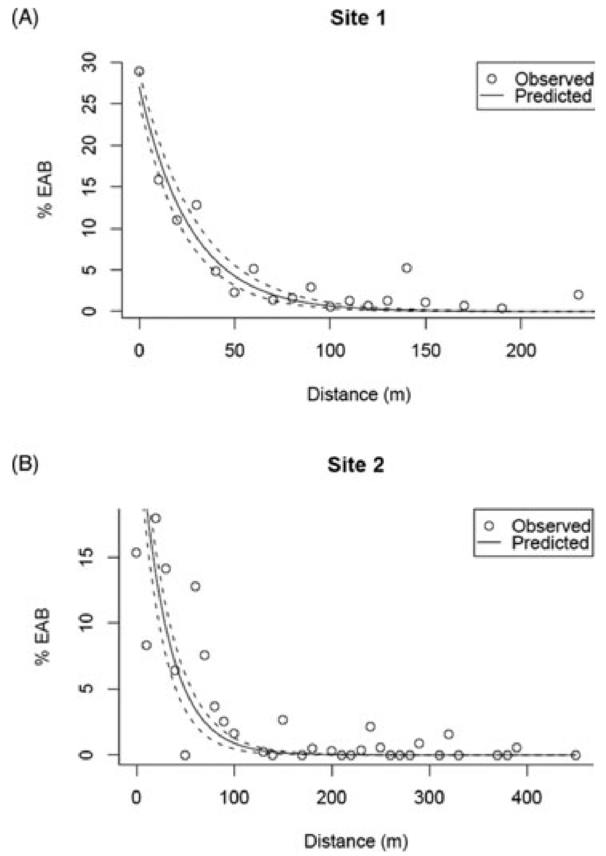

Figure 1 Percentage of *Agrilus planipennis* observed by 10-m intervals and predicted by the Negative Exponential Function for: (A) Site 1 and (B) Site 2. Dashed lines represent 95% confidence intervals.

Discussion

The present study represents a somewhat unusual investigation of dispersal in that it utilized sampling of multiple realizations of successful oviposition events and larval development, rather than using artificial traps, as is typical of most studies. Passive interception techniques are most likely ineffective at low densities and active monitoring techniques are likely to influence the dispersal of organisms. For example, ash trees stressed by girdling or physical injury are often used to sample adult *A. planipennis* populations, but can alter dispersal behaviour over ranges of at least 50 m in low-density infestations (N. W. Siegert and D. G. McCullough, unpublished data; Siegert *et al*., 2009).

An unexpectedly high proportion of larval galleries were located near the source point of both infestations. Female *A. planipennis* beetles must feed on ash leaves for at least 2 weeks before oviposition begins (Bauer *et al*., 2004). This period presumably provides ample time for dispersal away from the emergence point, and flight mill studies suggest that female beetles may be physiologically capable of flying 1.5 km/day for at least a few consecutive days (Taylor *et al*., 2006). Ash trees at both sites, however, appeared to be healthy and provided beetles with ample foliage for adult beetles to consume and suitable sites for oviposition, presumably providing little motivation for long-distance dispersal. Long-distance dispersal by some proportion of mated females may occur in at least some situations, although an extensive sampling effort would be required to detect such long-distance events.

The relatively short distance over which *A. planipennis* was observed to disperse in these sites is likely to enhance the probability of establishment from a single introduction. In addition to the number of colonists in the founding population, the dispersal behaviour of a species can strongly affect the probability of establishment (Liebhold & Tobin, 2008; Robinet & Liebhold, 2009). Allee effects significantly affect the likelihood of establishment of low-density populations (Liebhold & Tobin, 2008) and factors that contribute to maintaining a higher local population density can increase the likelihood of successful establishment.

The short-distance dispersal patterns observed at both sites were reasonably well described by the negative exponential function (NEF). However, it should be noted that the approximately linear spatial arrangement of ash trees at the two sites may have effectively functioned as a corridor to facilitate *A. planipennis* dispersal. Whether *A. planipennis* dispersal patterns are similar in areas where ash distribution is patchy or locally absent is not known. Despite these limitations, we consider that the NEF using the parameterization described in Table 1 provides a useful description of the local dispersal of *A. planipennis*.

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References

Bauer, L.S., Haack, R.A., Miller, D.L., Petrice, T.R. & Liu, H. (2004) Emerald Ash Borer Life Cycle. *Emerald Ash Borer Research and Technology Development Meeting, 30 September to 1 October 2003*, Port Huron, Michigan.

Bolker, B.M. (2008) *bbmle: Tools for General Maximum Likelihood Estimation*. R package, Version 0.8.2 (http://www.cran.r-project.org/).

Bolker, B.M. (2009) *Ecological Models and Data in R*. Princeton University Press, Princeton, New Jersey.

Cappaert, D., McCullough, D.G., Poland, T.M. & Siegert, N.W. (2005) Emerald ash borer in North America: a research and regulatory challenge. *The American Entomologist,* **51**, 152–165.

EAB Info (2009) http://www.emeraldashborer.info [accessed 26 January 2009].

Liebhold, A.M. & Tobin, P.C. (2008) Population ecology of insect invasions and their management. *Annual Review of Entomology,* **53**, 387–408.

McCullough, D.G., Poland, T.M. & Cappaert, D. (2009) Emerald ash borer (*Agrilus planipennis*) attraction to ash trees stressed by girdling, herbicide or wounding. *Canadian Journal of Forest Research,* **39**, 1331–1345.

R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Austria.

Robinet, C. & Liebhold, A.M. (2009) Dispersal polymorphism in an invasive forest pest affects its ability to establish. *Ecological Applications,* **19**, 1935–1943.

Shigesada, N. & Kawasaki, K. (1997) *Biological Invasions: Theory and Practice*. Oxford University Press, New York, New York.

Siegert, N.W., McCullough, D.G., Williams, D.W., Fraser, I. & Poland, T.M. (2009) Dispersal of *Agrilus planipennis* (Coleoptera: Buprestidae) from discrete epicenters in two outlier sites. *Environmental Entomology,* in press.

Taylor, R.A.J., Poland, T.M., Bauer, L.S. & Haack, R.A. (2006) Is emerald ash borer an obligate migrant? *Emerald Ash Borer Research and Technology Development Meeting, 26–27 September 2005*, Pittsburgh, Pennsylvania.

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