



Monitoring the impact of introduced emerald ash borer parasitoids: factors affecting *Oobius agrili* dispersal and parasitization of sentinel host eggs

Nicole F. Quinn · Jian J. Duan · Joseph Elkinton

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Abstract Emerald ash borer (EAB) *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae) is an invasive, wood-boring pest of North American ash trees (*Fraxinus* spp.). *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), a solitary egg parasitoid, was one of the several parasitoids introduced from the pest's native Northeast Asian range to the USA for EAB classical biocontrol. Since its introduction, this agent has been released over 31 states against EAB, yet determination of the spread and impact of this parasitoid has proved difficult partly because of its small size and cryptic host eggs. The present study examines the dispersal distance and parasitism of *O. agrili* shortly after release, as well as the impact of host's food plants (trees), where the host eggs were deployed. Sentinel EAB eggs were deployed on pairs of green ash (*Fraxinus pensylvanica*) and white fringe (*Chionanthus virginicus*) trees in circles around the release point up to 45 m away. After 48 or 120 h, the eggs were retrieved and examined for parasitism. There was no significant difference in observed

parasitism by distance or tree species. However, significantly more EAB eggs were parasitized in the longer deployment compared to the shorter deployment. These findings suggest that sentinel EAB eggs may be deployed on ash or white fringe trees to effectively monitor the establishment and spread of *O. agrili*. Future studies using sentinel host eggs in natural ash stands may yield further insights into the spread rate of *O. agrili* post-release and its effectiveness in suppressing the targeted pest populations over time.

Keywords Biological control · Dispersal · Invasive species · Parasitoid · Sentinel host

Introduction

Factors affecting insect establishment and dispersal after deliberate and unintentional introduction to new areas have been perennial topics of investigation. Failure to establish and spread can be caused fully or in part by many biotic and abiotic variables, including but not limited to: phenological mismatch (Ramsfield et al. 2016), insufficient propagule size and number (Lockwood et al. 2005), unavailability of hosts (Dang et al. 2021), extreme weather events (Tobin et al. 2017; Macquarrie et al. 2019), stochasticity and Allee effects (Williams et al. 2021), lack of habitat connectivity (Lustig et al. 2017), and dispersal ability (Fagan et al. 2002; Fahrner and Aukema 2018). In

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N. F. Quinn (✉) · J. J. Duan
Beneficial Insects Introduction Research Unit, USDA
ARS, 501 South Chapel St., Newark, DE 19713, USA
e-mail: nfquinn@umass.edu

N. F. Quinn · J. Elkinton
Department of Environmental Conservation, University
of Massachusetts Amherst, 160 Holdsworth Way, Amherst,
MA 01003, USA

the context of classical biological control, determining the dispersal capacity of introduced insects is an essential aspect of selecting agents and predicting their subsequent establishment and spread. A balance between high and low dispersal ability must be sought in order to avoid the potential pitfalls of slow spread, inbreeding, and Allee effects (Heimpel and Asplen 2011). Due to the myriad factors potentially affecting dispersal and establishment, each insect of interest must be studied on a case-by-case basis.

Agrilus planipennis Fairmaire (Coleoptera: Buprestidae), or emerald ash borer (EAB), is among the most damaging invasive species in North America (Herms and McCullough 2014). The larval stage of EAB feeds on the phloem of ash trees (*Fraxinus* spp.), resulting in tree decline and eventual death (MacFarlane and Meyer 2005). Since its accidental introduction in Michigan, USA in 2002, it has invaded 35 US states and five Canadian provinces, causing severe economic losses and degradation of forest ecosystem functions and services (Kovacs et al. 2010; McCullough 2019). Besides utilizing *Fraxinus* spp. trees as food plants in both native and newly invaded ranges, this beetle has recently been discovered successfully attacking the white fringe tree, *Chionanthus virginicus*, native to the southern USA (Peterson and Cipollini, 2017; Olson and Rieske 2019).

Classical biological control is among the most promising long-term, low-cost methods through which to regulate invasive EAB populations (Bauer et al. 2015; Duan et al. 2018). To this end several parasitoid species from EAB's native range were collected, tested, and selected for introduction to North America. One of these parasitoids was *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae). In its native range, *O. agrili* is responsible for 12–62% EAB egg mortality in infested ash trees (Liu et al. 2007). As an egg parasitoid, *O. agrili* prevents damage to ash trees by attacking EAB before they hatch and begin feeding on the trees (Liu et al. 2007). Since its release in North America, *O. agrili* attack rate on EAB infesting ash trees have been low and variable, but they have been observed to parasitize up to 21.8% of eggs (Abell et al. 2014; Duan et al. 2015). Currently, it is not known if *O. agrili* attacks host eggs laid on white fringe trees. Thus, there is a need for further study of factors affecting *O. agrili* performance.

The uncertainties around *O. agrili* parasitism rates are due in part to the difficulty in sampling this minute

insect. Visual surveys for EAB eggs are possible, but observer effects are a concern (Abell et al. 2014; Jennings et al. 2018). Many studies of *O. agrili* utilize bark sifting, in which the bark of ash trees is removed and EAB eggs sifted out and examined for evidence of parasitization (Abell et al. 2014; Jennings et al. 2018; Petrice et al. 2021). This method is considered to be among the most effective (Petrice et al. 2021). Yellow pan traps are another commonly used method, and while the success rate is mixed, yellow pan traps do successfully capture *O. agrili* (Parisio et al. 2017; Petrice et al. 2021). A fourth sampling method, sentinel eggs, is effective, but requires laboratory production of EAB eggs in sufficient numbers and continued monitoring of the eggs after deployment (Duan et al. 2011, 2012; Jennings et al. 2014; Petrice et al. 2021). However, sentinel eggs have the benefit of providing quantitative measures of parasitoid activity and efficacy (% parasitism), as opposed to the other methods, which either: (1) focus on the detection of adults in the case of yellow pan traps, or (2) estimate biocontrol activity based on the number of eggs sampled via bark scraping or peeling where initial number of eggs present in a given year is unknown, making it difficult to accurately calculate annual percent parasitism (Duan et al. 2012). As such, developing a better understanding of the efficacy of sentinel eggs as a sample method, as well as potential ways to improve this method, are needed.

An important aspect of developing an effective classical biological control program is to determine the rate of establishment and spread of the released agent. This helps ensure sufficient propagule pressure for establishment, essential aspects of biological control (Wittmann et al. 2014). However, detecting the presence of an introduced species can prove challenging depending upon the species in question and the methods implemented (Caton et al. 2022). Compared to other EAB biocontrol agents, there are few studies of *O. agrili* establishment, efficacy, and dispersal in the field. Abell et al. (2014) collected relatively few *O. agrili*-parasitized eggs via bark sifting, but observed greater parasitization at release sites compared to control sites where releases had not taken place (18.9–21.8% vs. 3.3–4.3%, respectively), with most release and control sites located approximately 1 km apart and first detections occurring three years post-release in control sites. In a study of *O. agrili* establishment in Maryland, USA *O. agrili* was only

recovered from three out of nine release sites sampled after several years of repeated releases in those areas, suggesting poor establishment or detection (Jennings et al. 2018). There have been even fewer studies examining *O. agrili* rate of spread at finer scale. In one such study, Parisio et al. (2014) recovered *O. agrili* in yellow pan traps located up to 20 m away from the release point in a wooded area during a five week period of sampling. In New York, USA no *O. agrili* were captured in yellow pan traps deployed at 250 m intervals along a river leading away from release sites (Jones et al. 2019). To maximize *O. agrili* establishment and spread, we must determine factors affecting the dispersal and parasitism rate of *O. agrili* when released into the field. To this end, the present study determined the short-term dispersal of newly released adult *O. agrili* using sentinel host eggs deployed on different host trees at various distances from the release point.

Materials and methods

Study site and trees

This study took place in a large, mowed grass field located at the USDA-ARS Beneficial Insects Introduction Unit in Newark, DE, USA (39.66812° N, 75.74087° W) from June through July 2021 on sunny,

calm days (precipitation=0–0.36 cm, maximum wind=0–28.97 km h⁻¹, temperature=11.11–35.6 °C). The grass field (~2 ha) is also neighboring several small urban forests (0.5–1 ha) consisting of primarily maple (*Acer* spp), birch (*Betula* spp), and ash (*Fraxinus* spp.). A total of 21 green ash (*Fraxinus pennsylvanica*) and 21 white fringe tree (*Chionanthus virginicus*) saplings were used in this study (diameter at breast height 3–5 cm). Of these trees, four green ash and three white fringe trees were planted at the edge of unmanaged wooded areas, while the rest were potted. All trees were deployed in pairs (one green ash and one white fringe tree). Figure 1 depicts our plot design. At the center of the study area, a pair of trees was designated as the release trees, where parasitoid releases would occur (Fig. 1a). Tree pairs were placed at various distances (9–45 m) away from the pair of central release trees in modified concentric circles as follows: 9.6 ± 0.4 m ($n=4$), 20.0 ± 1.2 m ($n=6$), and 34.6 ± 2.5 m ($n=10$). Trees within the same pair were approximately 0.5–1.0 m apart (Fig. 1b).

Insects

All insects were reared at the USDA-ARS Beneficial Insects Introduction Unit in Newark, DE, USA. EAB eggs were produced as described in Duan et al. (2013). Host eggs used in this experiment were 0–4 days old, well within the window of susceptibility



Fig. 1 **a** Overview of the study design. At the center of the study area, a pair of trees was designated as the release trees, where parasitoid releases would occur. Sentinel eggs were not deployed at the release trees. Tree pairs on which sentinel egg pouches were deployed were placed at various distances (9–45 m) away from the pair of central release trees (red pin) in modified concentric circles. Trees in group A (green pins)

were 9.6 ± 0.4 m from the release point ($n=4$), trees in group B (yellow pins) were 20.0 ± 1.2 m ($n=6$) from the release point, and trees in group C (blue pins) were 34.6 ± 2.5 m ($n=10$) from the release point. **b** A view of the release trees and several of the trees on which sentinel eggs were deployed. Trees within the same pair were approximately 0.5–1.0 m apart

and acceptability for *O. agrili* (Duan et al. 2014). *Oobius agrili* used in this experiment were from a continuously reared culture of field-collected *O. agrili* that were originally collected in Northeast China between 2008 and 2010 (Duan et al. 2014).

Sentinel egg deployment and parasitoid release

EAB eggs oviposited on coffee filter paper were used as sentinel host eggs in this experiment. The filter paper was cut into strips containing 10–20 eggs, or several smaller strips adding up to that number of eggs, with the same number of eggs per pouch used in a given trial. The eggs were then placed in 8×10 cm mesh (1 mm aperture size) pouches. One sentinel egg pouch was attached to each tree via garden wire at approximately breast height. Sentinel eggs were not deployed on the central release trees. Approximately 200–320 adults of *O. agrili* were released at the central release trees by opening the vials in which they were contained, placing the vials at the base of the release trees, and allowing the parasitoids to leave the vials of their own volition. Sentinel host eggs remained in the field for either 48 h (n=3) or 120 h (n=2) post *O. agrili* releases. At the end deployment, sentinel host eggs were retrieved from the field and then maintained in the laboratory under normal rearing conditions (25 °C, 65% RH, L:D 16:8) for approximately four weeks to evaluate parasitism. The number of remaining undamaged, parasitized, and predated eggs was recorded according to methods described in Liu et al. (2007) and Duan et al. (2012). Egg parasitism was scored based on successful development of parasitoid larvae, which were associated with darkening host eggs. Eggs were considered predated if visible evidence of the egg being consumed was present (i.e., egg was visibly pierced or chewed or fragments of chorion present). Trials were separated by at least one week.

Statistical analysis

All data were analyzed using SAS JMP Pro 15.1.0 (SAS Corporation, Cary, NC, USA). The proportion of eggs parasitized per pouch were analyzed via likelihood ratio χ^2 test based on generalized linear (binomial logit link) model, with distance from release tree, tree species, and deployment time as covariables.

Results

Overall, $22.6 \pm 2.0\%$ of sentinel eggs deployed were parasitized by *O. agrili*. Parasitism was observed throughout the deployment distances sampled, including the farthest distance, 44.8 m from the release point in both the 48 and 120 h trials. No significant effect of distance from release point on proportion of sentinel host eggs parasitized by *O. agrili* was observed ($\chi^2=1.89$, $df=1$, $P=0.17$) (Fig. 2). There was no significant difference in the rate of parasitism between eggs deployed on green ash and white fringe trees ($\chi^2=0.05$, $df=1$, $P=0.83$) (Fig. 3a). However, parasitization was significantly greater in EAB eggs that were deployed for 120 h compared to those that were only deployed for 48 h ($\chi^2=10.91$, $df=1$, $P=0.001$). Parasitism after 120 h deployment (mean= $29.4 \pm 3.0\%$) was nearly double that of the parasitism observed after 48 h (mean= $16.0 \pm 2.4\%$) (Fig. 3b). We also observed losses of deployed eggs due to undetermined predators throughout the study. However, the rate of predation was relatively low, with $\sim 15.8 \pm 1.6\%$ of eggs predated.

Discussion

Our study found that while tree species and distance from the release point did not affect parasitism, *O. agrili* can travel as far as 45 m in as little as 48 h after release to parasitize eggs. This suggests that the potential rate of spread after release is much greater than previously thought (e.g. Abell et al. 2014) and not necessarily constrained by tree species or linear distance. These findings potentially allow for greater

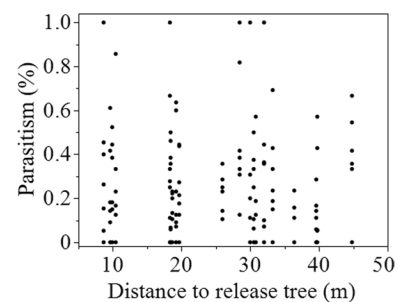
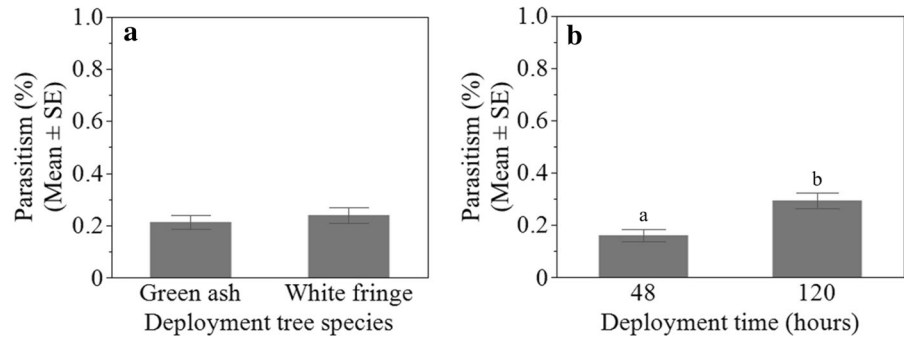


Fig. 2 Proportion of eggs parasitized by *O. agrili* by distance (m) away from the release point. No significant difference in parasitization among distances was observed ($P > 0.05$)

Fig. 3 Mean \pm SE proportion of eggs parasitized by *O. agrili*: **a** by tree species on which the eggs were deployed (green ash or white fringe tree), and **b** deployment time (48 or 120 h). Significance ($P < 0.05$) within subfigures is indicated by letters. Absence of letters indicates $P > 0.05$



flexibility in the design of sampling schemes using sentinel host eggs. Future studies should continue to expand the radius of the study area and allow at least 120 h field exposure of deployed sentinel host eggs after the parasitoids are released to determine the maximum distance (or capacity) of the parasitoid dispersal and establishment.

A longer sampling window would allow the parasitoids more time to search for and attack host eggs, but would limit the precise determination of rate of spread for several reasons. More time in the field may allow for greater opportunity for predation (Jennings et al. 2014), reducing the accuracy of the estimate for in-field parasitism. Predation rates of wild EAB eggs can be as high as 37–52% in the field (Duan et al. 2011). Jennings et al. (2014) found that predation can be reduced by almost 40% compared to unprotected controls through using 1 mm aperture mesh pouches with no significant reduction in parasitism. Similar pouches were used to protect sentinel eggs from field predation in our study, but still resulted in ~15.8% sentinel eggs preyed upon by identified predators. Further investigation into factors that may affect predation, such as pouch deployment method, tree species, and local variation is underway (Quinn and Duan unpublished).

In addition to loss of sentinel eggs due to predation during field exposure, host suitability also decreases over time, with eggs older than two weeks being unsuitable for parasitization (Duan et al. 2014), further limiting the benefits of longer deployment. Reducing the sampling duration (i.e., the amount of time sentinel eggs exposed to the field conditions) may help determine the rate of *O. agrili* spread after release. In laboratory studies, an individual *O. agrili* will attack an average of 19–24 eggs in the first week after emergence at 25 °C, but the attack rate

sharply reduces to less than five eggs after the third week (Hoban et al. 2016). The number of parasitoids released (200–320) relative to the host eggs deployed in each replicate (420–840) was approximately 1:3. This suggests that the reduced parasitism observed in the shorter duration trial is not due to the parasitoid ovipositional limit, but rather host finding or dispersal limits. Another consideration when applying our findings to field populations is that a natural, forested environment is more heterogeneous than our study design, which may complicate host finding on a local scale (Bukovinszky et al. 2007), but improve biological control at a landscape level (Cohen and Crowder 2017; Boses Baillod et al. 2017). Cues, semiochemical or otherwise, used by *O. agrili* to locate *A. planipennis* eggs are currently unknown, although the volatile profiles of *A. planipennis* tree hosts have been documented (Pureswaran and Poland 2009; Peterson et al. 2020) and may be attractive to natural enemies of the emerald ash borer. Further study of *O. agrili* behavior in both laboratory and natural settings could provide a better understanding of factors affecting *O. agrili* host finding.

Ever since the documentation of successful use of *C. virginicus* as an alternate host (Cipollini 2015; Peterson et al. 2020), there have been concerns about the potential of *C. virginicus* to serve as an enemy free space for *A. planipennis* (Olson and Rieske 2019). Our study found no difference in parasitization between eggs deployed on *F. pennsylvanica* and *C. virginicus*. While investigations into tritrophic interactions of *A. planipennis*, its parasitoids, and its host trees (both new and old) are still warranted, our study may provide some measure of reassurance that, at least in the case of *O. agrili*, biological control activity may not be compromised should *A. planipennis* oviposit on *C. virginicus*. However, this remains

to be verified in the field for the larval parasitoids, *S. galinae* and *T. planipennisi*. Recent laboratory studies suggest that both *S. agrili*, *S. galinae* (Ragozzino et al. 2021), and *T. planipennisi* (Hoban et al. 2018) performance is only moderately affected by host plant, further suggesting that host plant effects on biological control may be limited.

It is important to note that abiotic factors such as wind and rain can strongly impact parasitoid dispersal and activity (Weisser et al. 1997; Kristensen et al. 2013). However, given that throughout each trial maximum observed windspeed remained at 18 km h⁻¹ or less, precipitation was minimal (<1 cm), and temperatures were within historical norms for the time of year, it is unlikely that abiotic conditions adversely affected parasitoid foraging or dispersal in this study. Future studies examining the impact of environmental conditions on parasitoid performance will be key, especially given the potential impacts of climate change on biological control agents and our ecosystems (Furlong and Zalucki 2017).

Overall, our study has demonstrated the efficacy of sentinel host eggs in determining the spread and realized parasitism rates of *O. agrili* immediately after environmental release. Continued studies of parasitism, in conjunction with other sources of EAB mortality such as predation, throughout their introduced range over time will be needed to determine long-term biological control contribution. Future studies should seek to determine the efficacy and activity of *O. agrili* at finer distance resolution through intensive studies on foraging behavior and chemical ecology. This will improve our understanding of factors affecting this important biological control agent's impact on *A. planipennis*.

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Declarations

Conflict of interest The authors have no relevant financial or non-financial competing interests to disclose.

Ethical approval The authors have no relevant financial or non-financial competing interests to disclose. This work was done in compliance with all BioControl ethical standards.

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Dr. Nicole F. Quinn has been a postdoctoral research associate in the Department of Environmental Conservation at the University of Massachusetts, Amherst working with Joseph Elkinton (UMass Amherst) and Jian Duan (USDA ARS) since 2020. The focus of her postdoctoral studies has been the biological control of emerald ash borer. Previously, she has worked on habitat management to enhance beneficial insect activity in cucurbit agroecosystems, as well as the biological control of the brown marmorated stink bug in the woodland-orchard interface by *Trissolcus japonicus* and other parasitoids.

Dr. Jian J. Duan is the lead scientist at ARS Beneficial Insects Research Introduction unit on biological control of invasive wood-boring insects such as emerald ash borer and Asian longhorned beetle. He has played a critical role in developing, evaluating, and implementing the current emerald ash borer biological control program in the U.S., and first demonstrated the significant impacts of introduced natural enemies on the emerald ash borer population dynamics and ash sapling survivor and recovery in the aftermath of emerald ash borer invasion.

Dr. Joseph S. Elkinton is a professor in the Department of Environmental Conservation at the University of Massachusetts, Amherst. He specializes in the study of the ecology, population dynamics and biological control of invasive forest insects. He has been part of the team evaluating and implementing the biocontrol-based areawide management program against emerald ash borer in Northeastern US since 2015, working closely with Jian Duan of ARS.