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Postrelease assessment of *Oobius agrili* (Hymenoptera: Encyrtidae) establishment and persistence in Michigan and the Northeastern United States

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The emerald ash borer (EAB), *Agrilus planipennis* Fairmaire (Coleoptera: Buprestidae), is an invasive woodboring pest of ash trees (*Fraxinus* sp.) in North America. Among the Asiatic parasitoids being released for the management of EAB in North America, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae) is the only EAB egg parasitoid. To date, more than 2.5 million *O. agrili* have been released in North America; however, few studies have examined its success as a biological control agent of EAB. We conducted studies to assess *O. agrili* establishment, persistence, spread, and EAB egg parasitism rates in Michigan at the earliest release sites (2007–2010), as well as at more recent release sites (2015–2016) in 3 Northeastern United States (Connecticut, Massachusetts, New York). In both regions, we documented successful *O. agrili* establishment at all but one release site. In Michigan, *O. agrili* has persisted at release sites for over a decade and spread to all control sites located 0.6–3.8 km from release sites. Overall, EAB egg parasitism ranged from 1.5% to 51.2% (mean of 21.4%) during 2016–2020 in Michigan and from 2.6% to 29.2% (mean of 16.1%) during 2018–2020 in the Northeastern states. Future research efforts should focus on factors affecting the spatiotemporal variation in EAB egg parasitism rates by *O. agrili*, as well as its potential range in North America.

Key words: biological control, parasitoid, invasive species

Introduction

Agrilus planipennis Fairmaire (Coleoptera: Buprestidae), or emerald ash borer (EAB), is an invasive woodboring pest of ash trees (*Fraxinus* sp.) and is among the most injurious invasive forest pests in North America. Ash is a diverse and abundant genus in North American forest ecosystems and the widespread mortality caused by EAB is causing ecological harm (Flower et al. 2013, Klooster et al. 2018, Ward et al. 2021). Ash tree treatment and removal costs combined with resource losses to forest-dependent industries have exceeded $10.7 billion (Kovacs et al. 2010, Herms and McCullough 2014). Although insecticidal trunk injections can be extremely effective at protecting individual trees from EAB infestation, this approach is challenging to employ for landscape-scale management (Mota-Sanchez et al. 2009, McKenzie et al. 2010, Smitley et al. 2010, McCullough et al. 2011). As a result of the rapid spread of EAB, limited impacts from native natural enemies, and challenges posed when suppressing EAB infestations through other means, a classical biological control program was formally initiated in 2007 (Bauer et al. 2015, Duan et al. 2018). Ultimately, biological control may provide a long-term, low-cost, and environmentally acceptable approach to the reduction of EAB population densities below a tolerance threshold for native ash tree growth, survival, and reproduction in North America (Bauer et al. 2015, Margulies et al. 2017, Duan et al. 2018, 2023, Kashian et al. 2018).

Table 1. Location, release history, and distance of release plots from control plots (Michigan only) at *Oobius agrili* release study sites[a]

State	Site code[b]	Latitude	Longitude	Release years	Total individuals released	Distance (km) to control
Michigan	LP	42.69999	84.37634	2008, 2009	500	0.7
	CP	42.73083	84.42282	2007, 2008, 2009	1,330	1.0
	BF	42.5886	84.59602	2008, 2009	500	0.6
	RL	42.81593	84.34569	2010	1,160	3.8
	GSW	43.20812	84.44715	2009, 2010	1,375	2.8
	MRE	43.14650	84.54349	2010	1,165	9.1
Connecticut	CT1	41.65792	73.01888	2015, 2016	1,300	
	CT2	41.65894	73.02096	2015, 2016	1,300	
	CT3	41.93702	72.54760	2015, 2016	1,300	
Massachusetts	MA1	42.48844	73.11227	2015, 2016	2,200	
New York	NY1	42.00367	73.90917	2015, 2016	1,340	
	NY2	42.11884	−73.88778	2015, 2016	1,500	

[a]There is no “distance to control” for the northeast sites provided due to the fact that releases occurred at all of these sites.
[b]LP, Legg Park and Harris Nature Center; CP, Central Park and Nancy Moore Park; BF, William M. Burchfield Park; G RL, Rose Lake State Wildlife Area; SW, Gratiot-Saginaw State Game Area; MRE, Maple River State Game Area;CT1, Mattatuck State Forest One; CT2, Mattatuck State Forest Two; CT3, Cromwell Wildlife Management Area; MA01, Dalton State Conservation forest; NY1, Red Hook Conservation Forest; NY2, Dubac Farmland Wildlife Area.

After host range testing in quarantine, the egg parasitoid, *Oobius agrili* Zhang and Huang (Hymenoptera: Encyrtidae), along with 2 larval parasitoids, were first released in Michigan in 2007 (Bauer et al. 2015). After the development of the USDA EAB Biocontrol Program, parasitoid releases expanded throughout the invaded ranges of EAB in North America (Bauer et al. 2015, Duan et al. 2018, USDA–APHIS/ARS/FS 2019). To date, over 2.5 million *O. agrili* have been released in North America, spanning 31 states and the District of Columbia in the United States and 2 provinces in Canada. Of these, *O. agrili* parasitized eggs or adults have been recovered in 17 US states and both Canadian provinces (https://www.mapbiocontrol.org/).

Oobius agrili is a solitary multivoltine EAB egg parasitoid that has at least 2 generations per year (Liu et al. 2007). Reproduction is entirely thelytokous parthenogenetic with an average of 52 and 72 progeny produced per diapaused- and nondiapaused-female parasitoids, respectively (Duan et al. 2014b, Hoban et al. 2016, Larson and Duan 2016). *Oobius agrili* overwinter as facultative or obligatory diapausing prepupae within EAB eggs. Facultative diapause is induced when immature *O. agrili* larvae are exposed to photophases <14.5 h, while obligatory diapause occurs in a small proportion of progeny regardless of photophase length (Duan and Larson 2019, Petrice et al. 2019). Surveys of EAB natural enemies in the native range of *O. agrili* in Northeast China documented EAB egg parasitism rates of 12.0–43.8% (Liu et al. 2007). Postrelease studies in Michigan reported EAB egg parasitism by *O. agrili* to average 21.8% (Abell et al. 2014, 2016); however, research on the long-term establishment, parasitism rates, and impacts on EAB populations and ash health in its introduced range are ongoing due to the long life cycle of ash trees and the complexity of ecosystem dynamics in aftermath forests (Duan et al. 2017, 2023, Margulies et al. 2017, Kashian et al. 2018).

While several published studies have documented the establishment and impacts of introduced EAB larval parasitoids (Duan et al. 2013, 2019, 2021, 2023, Jennings et al. 2016, Jones et al. 2019, Aker et al. 2022), comparatively fewer studies are available on *O. agrili* establishment or impacts (Abell et al. 2014, 2016, Jennings et al. 2018). Given the number of *O. agrili* released throughout the invaded range of EAB in North America, better documentation of its establishment and impact is needed. The purpose of this study was to assess *O. agrili* persistence, spread, and EAB egg parasitism rates in Michigan, at some of the first EAB biocontrol release sites (2007–2010), as well as establishment and EAB egg parasitism at more recent release sites (2015–2016) in 3 Northeastern US states.

Materials and Methods

Study Sites

The study was conducted in 2 northern regions of the United States, including Michigan and the Northeastern US states of Connecticut, Massachusetts, and New York. In Michigan, study sites consisted of 6 secondary mixed-hardwood forests containing both green ash (*Fraxinus pennsylvanica* Marshall) and white ash (*F. americana* L.), where *O. agrili* was released from 2007 to 2010 (Table 1; Duan et al. 2013, Abell et al. 2014). Each Michigan site consisted of 2 plots, a plot where parasitoids were released and a control plot (located 0.6–9.1 km away) where no parasitoid releases occurred (Table 1). The 6 study sites in the Northeastern United States were also composed of secondary mixed-hardwood forests containing green and white ash trees and included 3 sites in Connecticut, 1 site in Massachusetts, and 2 sites in New York. Parasitoids were released at all Northeastern US sites from 2015 to 2016 (Table 1). Site code names, locations, years of releases and numbers of parasitoids released are presented in Table 1. Previously published studies provide additional site information including GPS coordinates, maps, background on EAB-invasion history, number and time of parasitoid releases, and general site characteristics such as ash tree species for the sites in Michigan (Duan et al. 2013, Abell et al. 2014) and the Northeast (Duan et al. 2019).

Sampling Procedures for EAB eggs and parasitism

In both Michigan (for EAB egg parasitism occurring in years 2016–2018 and 2020) and the Northeastern US sites (for EAB egg parasitism occurring in years 2018–2020), we sampled EAB eggs after the completion of the growing season for each sample year (i.e., during the fall–spring months) using previously described bark-scraping and sifting procedures (Abell et al. 2014, Jennings et al.2018, Petrice et al. 2021). Briefly, live ash trees with visible signs of EAB infestation (e.g., fresh woodpecker feeding holes, epicormic sprouts, and/or previous-year exit holes) were selected. At each site, except for Michigan sites for the 2020 EAB egg parasitism year, 5 trees were sampled using a draw knife to scrape or shear off a sample of outer bark onto a sheet of plastic or into a large plastic storage tote from an area of 2.5 × 100 cm at breast height (total = 250 cm^2) around the tree trunk (Petrice et al. 2021). Bark area sampled was increased to 1,000 cm^2 and 10 trees per site for the 2020 EAB egg parasitism year in Michigan. No samples were collected for egg parasitism that occurred in 2019 at Michigan sites due to the COVID-19 pandemic. Collected bark was stored in paper bags and allowed to dry for several weeks before it was sifted through a No. 14 soil sieve (after shaking). Sifted debris was inspected under a dissecting microscope, all EAB eggs were removed, and the fate of each egg was recorded (i.e., hatched, dead, parasitized with exit hole, or parasitized with dead parasitoid).

Analyses

Data were analyzed separately for each region using a generalized linear model with a binomial distribution (SAS Institute 2012). Degrees of freedom were calculated using the Kenward–Rodger method. Estimated marginal means (i.e., least squares means) that were significantly different (P < 0.05) were separated with Tukey–Kramer means comparison procedure (SAS Institute 2012). Bark samples lacking EAB egg recovery were not included in analyses.

For the Michigan data, the effects of year, site, plot treatment (i.e., parasitoid release plot or control plot), the interaction between plot treatment and year, and the interaction between plot treatment and site on the proportion of EAB eggs parasitized were tested. When interactions were significantly different, differences between plot treatments were analyzed separately for each sample year or site. The Maple River site (MRE) in Michigan was dropped from the analyses because *O. agrili* was not recovered at the release plot but was recovered from EAB eggs parasitized in 2020 in the control plot.

For the Northeastern data, the effects of year and site on the proportion of eggs parasitized were tested. The CT2 site was dropped from the analyses because no samples were collected in 2020. Degrees of freedom were calculated using the Kenward–Rodger method.

Results

A total of 1,221 EAB eggs were recovered at Michigan sites, of which 254 were parasitized by *O. agrili*. The overall mean percentage of EAB egg parasitism was 21.4 ± 2.5%. EAB eggs parasitized by *O. agrili* were recovered from all treatment and control plots for all sites, except for the Maple River (MRE) release plot. EAB egg parasitism varied significantly among years (F = 16.3; DF = 3, 155, P < 0.0001), but not sites (F = 1.58; DF = 4, 155, P = 0.184). *Oobius agrili* parasitism was highest in 2018 (mean ± SE = 51.2 ± 8.40%) and lowest in 2016 (1.50 ± 0.900%; Fig. 1). No significant effect was found for treatment (F = 0.390; DF = 1, 155; P = 0.533), but both the interactions of treatment and year (F = 4.34; DF = 3, 155, P = 0.00570) and treatment and site (F = 6.67; DF = 4, 155, P < 0.0001) were significant. EAB egg parasitism was similar between control and release plots in 2016 (F = 1.13; DF = 1, 34, P = 0.295) and 2018 (F = 2.08; DF = 1, 24, P = 0.163), significantly higher in release plots in 2017 (F = 10.43; DF = 1, 39, P = 0.00250), and significantly higher in control plots in 2020 (F = 5.80; DF = 1, 66, P = 0.0188; Fig. 1). EAB egg parasitism between control and release plots within sites was similar for the GSW site (F = 0.110; DF = 1, 37, P = 0.746) and RL site (F = 0.230; DF = 1, 28, P = 0.636); significantly higher in release plots for 2 sites, BF (F = 6.54; DF = 1, 31; P = 0.0157) and CP (F = 13.91; DF = 1, 29, P = 0.0008); and significantly higher in control plots for the LP site (F = 10.89; DF = 1, 36, P = 0.00230; Fig. 2).

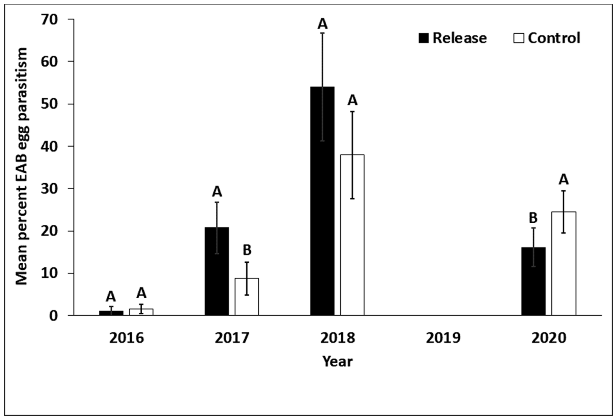

Fig. 1. Mean (± SE) EAB egg parasitism by *Oobius agrili* in Michigan study sites by treatment (release and no-release control) and year. Means within years with the same letters are not significantly different; Tukey–Kramer means comparison procedure (P < 0.05).

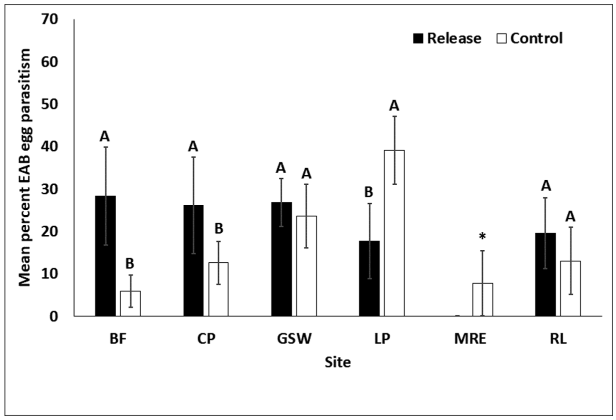

Fig. 2. Mean (± SE) EAB egg parasitism by *Oobius agrili* in Michigan by treatment (release and control) and site. Means within sites with the same letters are not significantly different; Tukey–Kramer means comparison procedure (P < 0.05). Site codes and locations are given in Table 1. *The MRE site was not included in model because *O. agrili* was not recovered at the release plot but had spread to control plot, presumably from another parasitoid release site that was not part of this study.

For the Northeastern US sites, a total of 550 EAB eggs were collected, of which 121 were parasitized by *O. agrili*. Overall mean parasitism was 16.1 ± 3.0%. EAB eggs were recovered from all sites in all 3 states. EAB egg parasitism varied significantly among years (F = 11.38; DF = 2, 91, P < 0.0001) and sites (F = 3.79; DF = 4, 91, P = 0.0067). EAB egg parasitism was lower in 2018 (3.2 ± 2.7%), compared with 2019 (26.2 ± 6.10%) and 2020 (21.2 ± 5.50%; Fig. 3). The percentage of EAB eggs parasitized was significantly higher at the MA site (28.9 ± 9.50%) compared with the NY1 site (12.1 ± 3.80%; Fig. 4).

Discussion

Success of the EAB biological control program hinges on the establishment and persistence of introduced parasitoids. The recovery of *O. agrili* parasitized EAB eggs over multiple years at all but one release site demonstrates that *O. agrili* is establishing in the Northeastern states and persisting and spreading in Michigan. EAB egg parasitism rates were variable across sites and years, and increased over time at the more recent release locations in the

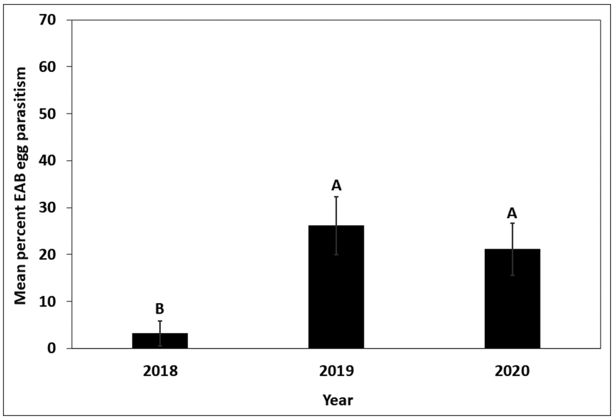

Fig. 3. Mean (± SE) EAB egg parasitism by *Oobius agrili* in the Northeastern US states of Connecticut, Massachusetts, and New York by sample year. Means with the same letters are not significantly different; Tukey–Kramer means comparison procedure ($P < 0.05$).

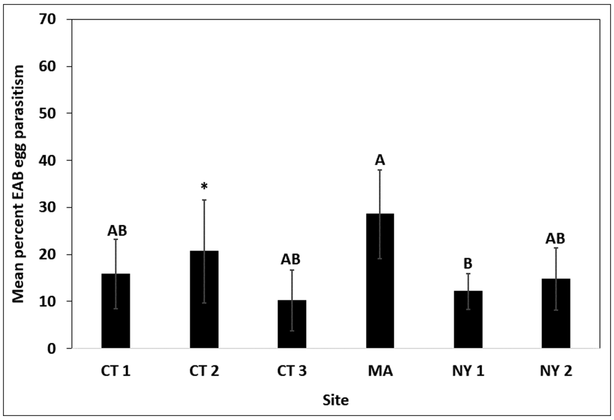

Fig. 4. Mean (± SE) EAB egg parasitism by *Oobius agrili* in the Northeastern US states of Connecticut (CT), Massachusetts (MA), and New York (NY) by study site. Study site codes and locations are given in Table 1. Means with the same letters are not significantly different; Tukey–Kramer means comparison procedure ($P < 0.05$). *The CT2 site was dropped from the analyses because no samples were collected in 2020.

Northeastern United States. At Michigan sites, where *O. agrili* has been established for over a decade, EAB egg parasitism was documented at all control sites, confirming it is spreading beyond release sites.

Several factors can affect *O. agrili* establishment and persistence including parasitoid–host synchrony, climate suitability, and photophase length (Jennings et al. 2014, Abell et al. 2016, Hoban et al. 2016, Petrice et al. 2019, 2020). For example, *O. agrili* only attacks EAB eggs <7 days old, requiring *O. agrili* adult emergence to be synchronized with EAB oviposition (Jennings et al. 2014). Furthermore, *O. agrili* is primarily bivoltine with most diapausing progeny produced by F_1 parents (Hoban et al. 2016, Larson and Duan 2016, Petrice et al. 2019). This requires synchronization of *O. agrili* F_0 adult emergence with the initiation of EAB oviposition to allow sufficient time for their progeny to emerge as F_1 adults and find suitable host eggs before EAB oviposition ends. A phenology model developed by Petrice et al. (2020) predicted that parasitoid–host synchrony remains relatively consistent across a range of latitudes in North America based on temperature alone. However, spatiotemporal variation in photophase length may limit *O. agrili* establishment and persistence in more southern latitudes (Larson and Duan 2016, Petrice et al. 2020). Similarly, Butler et al. (2022) found that 1–3 yr postrelease *O. agrili* established and persisted at 29% of Canadian release sites, which are further north than the sites sampled in our study but experience similar photoperiod and climate. Climate and photophase in Michigan and the Northeastern United States are similar to those in the native range of *O. agrili* in Northeast China, thus successful establishment of *O. agrili* in more southern latitudes remains uncertain.

Host densities could also affect *O. agrili* establishment and persistence. At our study sites in both regions, *O. agrili* were released when EAB populations were near peak densities, thereby increasing the probability of establishment. In Michigan, EAB populations declined rapidly in subsequent years due to diminishing ash–host resources and the establishment of other natural enemies, further reducing EAB populations (Duan et al. 2015, Kashian et al. 2018). In Michigan, EAB continues to persist but at much lower population levels that fluctuate annually (Duan et al. 2015, 2021, 2023). Despite the overall decline and annual fluctuations in EAB population densities in Michigan, *O. agrili* continues to persist at the study sites where it has been established for more than a decade (Abell et al. 2014, 2016). At the Northeastern US study sites, *O. agrili* parasitism rates increased relatively quickly within 2–3 yr after initial releases and reached rates similar to those at the Michigan sites.

Due to its small size, *O. agrili* was expected to disperse much more slowly than the introduced EAB larval parasitoids, which can spread several km per year (Jones et al. 2019, Rutledge et al. 2021, Aker et al. 2022, Quinn et al. 2022b). However, Quinn et al. (2022a) documented that *O. agrili* could disperse at least 45 m in 48 h. Working at the same Michigan sites as the current study, Abell et al. (2014) recovered *O. agrili* from some of the control plots as early as 3–4 yr after parasitoids were first released, including the GSW control plot, which is located 2.8 km from its respective release plot (Table 1). In the current study, EAB egg parasitism rates were still lower 12–15 years after *O. agrili* releases at 2 of the 5 Michigan control plots compared to their respective release plots, even though distances between plots were relatively short (Fig. 2, Table 1). On the other hand, parasitism rates at control sites were similar or higher than at the respective release plots for the other 4 sites with greater distances between the plots. These results suggests that *O. agrili* is capable of dispersing much farther than anticipated; however, it may take several years for populations to reach detectable levels. Increasing sampling efforts to include more sites over larger areas may provide some clarity on the extent of spread, and should be done before the parasitoids have spread over the entire landscape.

The overall *O. agrili* EAB egg parasitism rate of 21.4% recorded during this study in Michigan was very similar to that recorded by Abell et al. (2014) from release plots within the same sites in 2012–2013, indicating the parasitoid populations continue to persist in the release plots and have spread to control plots at these sites. Overall, parasitism rates in 2018 and 2019 at the Northeastern sites were similar as well. However, EAB egg parasitism rates varied considerably among years and sites and may be attributed to the functional response of *O. agrili* to spatiotemporal fluctuations in EAB densities, similar to those reported by Liu et al. (2007) in the insects' native range in Northeast China, and to undetermined environmental and site-specific factors. Similar variability in parasitism rates are reported for the established EAB larval parasitoids introduced as biocontrol agents at the same time at these study sites (Duan et al. 2015, 2023).

Although *O. agrili* alone may not be sufficient to suppress EAB populations, it does have 4 unique advantages over introduced larval parasitoids. First, as the only EAB egg parasitoid in North America, *O. agrili* is not impacted by intrinsic competition, which may occur among introduced and native North American EAB larval parasitoids, as well as woodpeckers, which target similar larval life stages (Cappaert and McCullough 2009, Duan et al. 2010, 2011, Duan et al. 2014a, Watt et al. 2016). Second, *O. agrili* is not constrained by tree bark thickness, as has been demonstrated for introduced larval parasitoids (Abell et al. 2012, Duan et al. 2021), given that EAB eggs are laid on the exterior of trees. Third, because *O. agrili* is thelytokous parthenogenetic, it is less impacted by Allee effects associated with mate finding, which is beneficial for parasitoid establishment and persistence when EAB populations are very low. Fourth, egg parasitism kills the pest before it feeds on host phloem, preventing EAB larvae from causing long term and often irreversible damage to the tree's vascular tissue. Furthermore, early-instar EAB larvae are frequently killed by vigorous growth and host plant resistance (Duan et al. 2010, Jennings et al. 2015), and reduction in EAB densities by *O. agrili* egg parasitism before vascular tissue damage occurs may increase the ability of trees to elicit a defense response against newly hatched EAB larvae.

In summary, *O. agrili* is establishing and persisting in Michigan and Northeastern states that have similar climates to *O. agrili*'s native range. *Oobius agrili* is also dispersing, but at slower rates than introduced EAB larval parasitoids. Although overall EAB egg parasitism rates were relatively low, rates for some years were comparable to parasitism rates documented for introduced EAB larval parasitoids. Because of the additive EAB mortality contributed by *O. agrili* and the unique advantages that EAB egg parasitism have over EAB larval parasitism, *O. agrili* is expected to play an important role in the EAB biocontrol program. More studies are needed to determine factors affecting the spatiotemporal variation, potential distribution, and long-term performance of *O. agrili* in different regions of North America.

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Author Contributions

Nicole Quinn (Data curation-Equal, Formal analysis-Equal, Project administration-Equal, Validation-Equal, Visualization-Equal, Writing – original draft-Lead, Writing – review & editing-Lead), Toby Petrice (Conceptualization-Equal, Formal analysis-Equal, Investigation-Equal, Visualization-Equal, Writing – review & editing-Lead), Jonathan Schmude (Data curation-Equal, Investigation-Equal), Therese Poland (Conceptualization-Equal, Investigation-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal, Writing – review & editing-Equal), Leah Bauer (Conceptualization-Equal, Investigation-Equal, Project administration-Equal, Supervision-Equal, Writing – review & editing-Equal), Claire Rutledge (Conceptualization-Equal, Investigation-Equal, Resources-Equal, Supervision-Equal), Van Driesche (Conceptualization-Equal, Investigation-Equal), Joseph S. Elkinton (Conceptualization-Equal, Funding acquisition-Equal, Investigation-Equal, Resources-Equal), Jian Duan (Conceptualization-Equal, Data curation-Equal, Investigation-Equal, Methodology-Equal, Project administration-Equal, Resources-Equal, Supervision-Equal, Validation-Equal, Writing – review & editing-Equal)

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